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Food Habits and Economic Relations of the Turtles of Michigan with Special Reference to Fish Management¹

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Introduction

This report, based on a combination of field and laboratory studies, is one of a series dealing with predation on fresh-water fishes as related to the practical problems of fish yield (Lagler, 1937). Researches on the physical, chemical, and on the more familiar biological features of fresh-water communities need to be supplemented by studies on the role of predation in their dynamic economy. Although the reduction of populations of predatory and so-called "noxious" animals is a common fish management practice, it often has little scientific basis and is for the most part of unknown effect. It is the purpose of the present study to learn which turtles, if any, retard the production of fish, to experiment with methods of control, to establish "a clean bill of health" for deserving species, and to determine other economic relations of these reptiles.

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Josselyn Van Tyne, Thomas Hinshaw, and Milton B. Trautman aided in the identification of bird remains. Ruth Marshall determined the water mites and J. W. Leonard, most of the insects. Calvin Goodrich and Henry van der Schalie are responsible for the specific determinations of the mollusks. Karl E. Goellner identified the amphipods and many of the decapods and G. W. Prescott, the algae. Ralph Peacock and Ann Peacock contributed many turtle specimens. To these individuals and to the many others who helped in innumerable ways, I extend my sincere thanks.

Procedure.—Being primarily concerned with the effect of turtles on fish yield, I have emphasized the study of the more abundant and aquatic species.

¹ Contribution from the Institute for Fisheries Research of the Michigan Department of Conservation and from the Department of Zoology and the Museum of Zoology of the University of Michigan. Substantial financial aid was given this study by the American Wildlife Institute and the Associated Fishing Tackle Manufacturers.

I include also the accumulated data for the less extensively investigated spotted turtle, the more terrestrial wood turtle, and the box turtle.

Studies on the relationships between turtles and fishes and on turtles as an economic resource were made in the field, from April through October in 1937, and from May through September in 1938. During these periods many turtle specimens were collected for food analyses, mostly by means of turtle traps. The stomach and colon contents of these individuals were subsequently analyzed by the most practicable quantitative and qualitative methods similar to those described by Salyer and Lagler (1940). Volumes of food items in stomachs were measured by displacement of water in graduated cylinders; volumes for those in intestines were estimated.

For each turtle species summaries of the quantitative relations of foods eaten and their frequency of occurrence have been made. In addition annotated lists of food items are presented. In these lists details of the numbers, identity, condition, and sizes of food organisms found are given. These data are useful in the interpretation of the volumetric and frequency of occurrence percentages in the tables, since in the lists each food group is broken down into its component items. This analysis also serves to disclose more of the interactions between predator and prey (e.g., differential vulnerability of prey organisms) and between prey species themselves (e.g., buffer effects).

Analysis of the contents of the entire digestive tract was made when possible in preference to sole study of the materials in stomachs, intestines, or droppings. For turtles at least, investigations based on any of these alone are misleading because of: (1) persistence of hard parts of some animals, such as the exoskeletons of crayfish and insects; (2) differential rate of digestion of various materials ingested; and (3) the delayed digestion of cellulose. It is unfortunate that no information is extant regarding rate of digestion, daily food requirements, and periodicity of feeding for turtles. If it were, it would be possible to greatly extend the application of the current findings.

Published information on the species of turtles native to Michigan has been reviewed, but is not repeated in the accounts of each species. Most important references on turtles are readily available; many of these, in addition to those cited, are listed in the bibliography.

The nomenclature followed for turtles is that of Stejneger and Barbour (1939) except for the painted turtles which is after Bishop and Schmidt (1931) and Hartweg (MS). Plant names are from Fassett (1940) and fish names are after Hubbs and Lagler (1941).

Results of Correlated Field and Laboratory Studies

In this section each species of turtle is discussed in systematic sequence. Descriptions and general range are not given since they may be found in the works of Ruthven, Thompson, and Gaige (1928), Conant (1938), and others. Some knowledge of the distribution is important for an understanding of the extent of the area to which the data here presented may pertain; maps by Conant (1938) showing range in the United States are therefore reproduced,

with his permission. Distribution in Michigan is compiled from Ruthven, Thompson, and Gaige (1928), the unpublished data of Helen T. Gaige and Norman E. Hartweg, and from my collection records. Maps of the state are given for each species, to show locations and water types from which specimens were studied for food.

STERNOTHERUS ODORATUS (Latreille)—Musk Turtle

Range and Size.—In Michigan the musk turtle has not been recorded from waters north of Town Line 16 (a line running east and west through the southern part of Saginaw Bay) and is as yet unknown from several of the southern counties (Fig. 1). The musk turtle in this region averages less than five inches in carapace length; the largest males and females examined ranged from 114 to 121 mm. (4.5 to 4.8 inches) in horizontal carapace length.

Habitat and Habits.—An excellent account of the natural history of this preeminently aquatic turtle in the Ann Arbor, Michigan, region has been published by Risley (1933). To this fine study I can add new data on food habits.

The musk turtle has been found in the quiet waters of lakes, ponds, and slow-moving streams throughout its range. In Michigan I have collected it most commonly in those portions of lakes, or lagoon-like sections of rivers, where aquatic vegetation grows abundantly but not so densely as to impede greatly the movements of turtles on the bottom. Particularly favorable environments were the reedy, firm-bottomed areas of such lakes as Whitmore (Washtenaw County), Sherman (Kalamazoo County) and Wolf (Van Buren County). This turtle is doubtless more abundant than commonly assumed. It is unobtrusive, not only because of the luxuriant growth of the alga *Basilcladia* on the backs of many individuals, but also because of its predominantly nocturnal and secretive habits. Although individuals were seen foraging at all hours of the day, they appeared to be more active at night. Specimens collected by hand at night were usually moving over open bottom. Those taken in the daytime were most often hidden, at least partly, under some sheltering object.

Food and Feeding Habits.—The feeding activities of this turtle appear to be confined to its aquatic environment. Occasional feeding on land is reported by other investigators (Newman, 1906).

Newman (*loc. cit.*), Evermann and Clark (1920), and Risley (1933) have reported the scavenging habits of this turtle. On the basis of the lack of response of musk turtles, or of any other Michigan turtle, to putrefying bait in traps, it seems that such scavenging may have been overestimated. Musk turtles have been observed by me to feed readily on freshly dead material but to refuse animal flesh in advanced stages of decay. The word "scavenger," then, as used in the present paper, should be taken to mean feeding on dead, but not putrefied material.

My studies of the food of the musk turtle are based on 113 specimens which contained food either in the stomach or colon, or in both of these organs. These turtles were collected mostly during late summer months of

1937-38 from thirteen lakes, three rivers, and two fish cultural establishments in Michigan (Fig. 1). In the following report of the food habits, the findings for the considerable series of specimens from Whitmore and Sherman Lakes are discussed separately; individuals from the remaining lakes of the same general ecological province are grouped together; those from rivers form another group; and those from fish rearing stations yet another. A summary of the volumetric and frequency of occurrence relationships of the various food groupings (Table 1) and an annotated list of the numbers and kinds of organisms eaten follow.

Whitmore Lake.—Whitmore Lake, of glacial origin and lying in the Huron

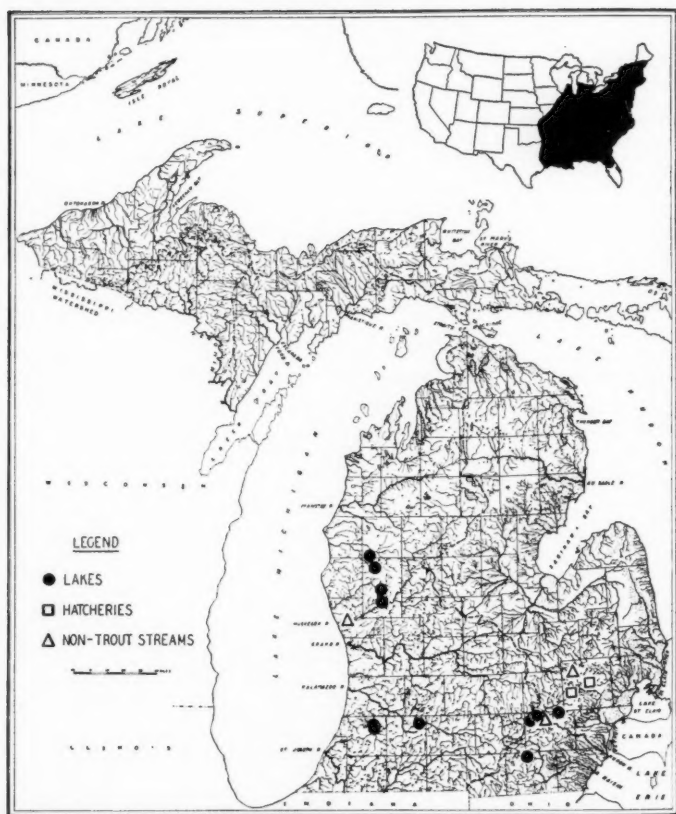


Fig. 1. Types and locations of waters from which musk turtles were studied and general range of the species in the United States.

River drainage, has a surface area of 677 acres and maximum depth in excess of fifty feet. The bottom is varied; sand, gravel, mud, and some marl appear extensively in the shoal areas. Several species of pondweed (*Potamogeton*), and hornwort (*Ceratophyllum demersum*), dominate the aquatic flora. Game and pan fishes present include largemouth bass (*Huro salmoides*), northern smallmouth bass (*Micropterus d. dolomieu*), yellow perch (*Perca flavescens*), common bluegill (*Lepomis m. macrochirus*), pumpkinseed (*Lepomis gibbosus*), and northern pike (*Esox lucius*). Associated with these are several species of minnows and other forage fishes, northern longnose gar (*Lepisosteus osseus oxyurus*), and bowfin (*Amia calva*).

The thirty-four musk turtles studied for food from this lake averaged 95 mm. (3.7 inches) and ranged from 70 to 115 mm. in length. They were collected in September and October of 1937. The stomachs of nineteen of these turtles contained food with a total volume of 2.7 cc. Thirty-two colons contained 28.0 cc. of food. These organs, in the remaining individuals of this series, and in several additional individuals collected from this lake in these months, were devoid of food. The snapping turtle, mid-western painted turtle and map turtle were also studied in Whitmore Lake.

In Whitmore Lake, in autumn, aquatic insects and their nymphs and larvae, snails, and carrion appear to be the most important food of this turtle. Fish carrion is more prominent in volume relationships in the stomachs than in the colons. Green plants, however, appear more prominently in colons than in the stomachs. Insects and snails comprise approximately the same proportion of the contents of both organs.

The aquatic insects most often taken were dragonfly nymphs and lepto-cerid caddis larvae, frequently *Leptocella albida*. Terrestrial insects were represented by eleven ants in one stomach, and by a larval lepidopteran in another.

The strong jaws with their broad occlusal surfaces appear to be correlated with mollusk- and seed-eating habits. For the most part, the mollusks and seeds of aquatic plants in the stomachs of this turtle are crushed beyond recognition.

All fish remains encountered were carrion. Earlier in the season, in July, when many more game fishes are killed, the species is even more a scavenger than in late summer. M. B. Trautman tells me that while fishing on this lake, he has observed musk turtles feeding on fish injured by anglers and also upon dead or dying bait "minnows" dumped from the fisherman's live-bucket.

Sherman Lake.—This lake is approximately one hundred acres in surface area (Henshaw, 1931), and has fairly extensive shoal areas with a bottom of sand, gravel, muck, and marl. The shores are hilly and partly open with meadows and partly wooded with some resort development, and much of the shore line is inaccessible by road. The dominant aquatic vegetation includes several large beds of *Nuphar advena* in the sheltered coves and species of *Potamogeton* in the more open waters. *Anacharis canadensis*, *Ceratophyllum demersum*, *Myriophyllum*, and *Chara* are common. Some bulrushes (*Scirpus*) and cattails (*Typha*) occur in a few restricted localities. Game and pan fishes present are largemouth bass, northern smallmouth bass, northern rock bass

(*Ambloplites r. rupestris*), several species of sunfishes (*Lepomis*), yellow perch and bullheads (*Ameiurus*). Minnows, darters, and a few eels (*Anguilla bostoniensis*) also occur.

The abundant and varied aquatic fauna and flora, the extensive shoal area with soft bottom, the limited resort development, the sandy banks and open meadows on much of the shore, and the absence of a marginal road favor the turtle population of this lake.

Food habits data for the musk turtle from Sherman Lake are based on 11.7 cc. of food contained in the stomachs of twenty-eight specimens. In length these turtles average 95 mm. (3.7 inches) and range from 60 to 110 mm. Excepting two individuals collected on August 20, 1937, all were taken from September 16-18, 1938. For comparison it should be noted that digestive tract contents of snapping, Blanding's, and mid-western painted turtles from this lake were also analyzed.

Insects, snails, and carrion appear as the most important foods of this turtle in Sherman Lake as in Whitmore Lake. The most common insects taken were leptoцерid caddis larvae and the most frequently encountered snails were *Helisoma* and *Ammicola*. Seeds of aquatic plants appeared rather abundantly. Carrion was found to be entirely the remains of fish. The single pan fish was a yellow perch $1\frac{3}{4}$ inches long, apparently alive when taken.

Miscellaneous lakes.—Thirty-five specimens collected throughout the two summers of field work in several lakes give a picture which substantiates those for Whitmore and Sherman Lakes. The average length of thirty-two of these turtles on which measurements were obtained is 98 mm. (3.9 inches); the range is 79 to 122 mm. The stomachs of twenty-one of these individuals contained 2.3 cc. of food for study and the colons of twenty-seven, 18.7 cc.

Insects, mollusks, and vegetable matter appear as the principal foods. The insects most frequently encountered were dragonfly nymphs and the mollusks were predominantly snails of the genera *Helisoma* and *Physa*. Crayfishes assume greater importance. As before, the vegetable matter encountered was very largely composed of the cracked or crushed seeds of aquatic plants.

Rivers.—The series of nine specimens available from sluggish river habitats gives results that strikingly resemble those for lakes. The average length for eight of these specimens was 99 mm. (3.9 inches); the range, 91 to 112 mm. Five contained a total of 1.0 cc. of food in their stomachs and seven had 4.7 cc. of such material in their colons.

Crayfishes assume somewhat greater significance in the food of musk turtles in this type of water. The insects eaten are again predominantly dragonfly nymphs, and the hard-coated seeds of *Nuphar advena* form the major part of the vegetable matter ingested.

Fish cultural establishments.—The series of eight specimens available for an appraisal of the status of the musk turtle at fish cultural stations is small. Excepting one specimen taken from a bluegill rearing pond at the Drayton Plains Hatchery on June 24, 1932, the turtles came from an ornamental and

forage fish rearing pond of the Sunset Water Gardens, near Milford, on September 26, 1937. The length of seven of these specimens was 89 to 97 mm., averaging 93 mm. (3.7 inches). Food was found with a total volume of 3.2 cc. in six stomachs and with a total volume of 2.0 cc. in four colons.

An estimated thousand and more bluegill larvae were taken by J. C. Salyer, II, from the stomach of an individual collected from a bluegill nest at the Drayton Plains state fish cultural station.

At the Sunset Water Gardens' pond, the food of the turtles hardly differs in any essential respects from that found on wild waters. The small pond from which the turtles were obtained contained many thousand young bluntnose minnows (*Hyborhynchus notatus*), topminnows (*Fundulus diaphanus*) and goldfish (*Carassius auratus*). Whether or not the eggs and larvae of these fishes are subject to musk turtle predation is not known, although presumably they may be eaten in some numbers during the bottom foraging and rooting activities of this small turtle. If one may base any conclusions on data so limited, it would seem that healthy adult and juvenile fishes are in general free from predation by musk turtles, even though they are very crowded and the turtles are possibly more numerous per unit area than in any natural water. No fish were found in the food of these specimens.

ANNOTATED LIST OF ITEMS IN THE FOOD OF 113 MUSK TURTLES

Game and pan fishes.—Such fishes were represented by one yellow perch 13¼ inches long, more than a thousand bluegill larvae (in a single turtle) and remains of two unidentified centrarchids. The bluegill larvae were in a specimen from a fish hatchery; the other items, in specimens from natural waters.

Unidentified fishes.—Remains of three unrecognizable fishes were found.

Carrion.—Remains of the bowfin, bluegill, pumpkinseed, and several centrarchids and unidentified fishes were recognized as carrion.

Leeches.—Two partially digested leeches were present.

Crayfishes.—Of the remains of 25 crayfishes (*Cambarus*), 2 were identified as *C. virilis*.

Insects.—In addition to fragmentary remains of many insects the following were determined: 6 mayfly nymphs including 1 *Caenis* and 2 *Hexagenia*; 1 grasshopper (*Melanoplus m. mexicanus*); *Anax junius*, *Leucorrhinia*, and *Celithemis* once each among the parts of 64 dragonfly nymphs; 6 damselfly nymphs, of which 1 was *Enallagma*; 3 Hemiptera, (*Ranatra*, *Pelocoris*, and a belostomatid); 11 beetles include 1 carabid, 3 dytiscids, 5 hydrophilids, 1 coccinellid, and 1 rhynchophoran; 298 caddisfly larvae of which 29 were unidentifiable and the remainder made up of 36 *Leptocella albida*, 232 lepto-cerids, and 1 limnephilid; 2 moth larvae of which 1 was a pyralid; 5 Diptera of which 2 were pupae and the remainder larvae of the groups Chironomidae, Stratiomyidae, and Brachycera; 13 Hymenoptera, 1 unidentified specimen and 11 winged ants (Formicidae), and 1 bee (*Apis mellifera*).

Snails and clams.—Of the mollusks found, the remains were largely bits

of almost completely decalcified shell. Only one could not be identified as to whether it was a snail or a bivalve. Snails recognized were 39 *Helisoma* (13 *H. trivolvis*, and 12 *H. antrosom*), 17 *Physa sayii*, 7 *Physa* sp., and 36 *Amnicola*. More than 20 additional snails were represented by soft parts only. Of several bivalves, 2 were *Pisidium*.

Plants.—Of the cryptogams, filamentous algae were the most common but miscellaneous colonial algae, *Chara*, and some mosses were also present. Phanerogams were often represented by fragments of leaves, stems, and seeds which lacked diagnostic properties and were therefore classed as "vegetable debris." Flowering plants occurred mostly as vegetative portions of the aquatics, *Potamogeton*, *Najas*, *Anacharis canadensis*, *Spirodela polyrrhiza*, *Ceratophyllum demersum*, *Ranunculus*, and *Utricularia*. Seeds of *Nuphar advena* numbered 69, of *Nymphaea odorata*, 29, and of *Bidens*, 4. One seed of a dogwood (*Cornus Amomum*) was also found.

SUMMARY AND CONCLUSIONS

That the musk turtle is an omnivore is conclusively demonstrated (Table 1 and Fig. 6). Stray insects, such as grasshopper, terrestrial beetles, the lepidopteran larva, and the bee and ants, are doubtless taken after they fall into the water, and thus do not affect the conclusion that this turtle is essentially aquatic in its feeding habits.

Although a few fishes are eaten, this so-called damage may be more than counterbalanced by feeding on other "enemies" of fish. Such insects as the predacious belostomatids and diving beetles may be placed in this category. Seeds of the "beggar-tick" (*Bidens*) appear to be injurious to fishes (Leonard, 1938).

Excepting possible harm by predation at hatcheries and on eggs and larvae of desirable species of fishes, it would seem that the principal adverse effects of the musk turtle on fish populations may be in the numbers of fish-food organisms that it eats. Benefits may accrue from its scavenging habits, its consumption of mosquito larvae, its destruction of mollusks that figure in the life cycles

TABLE 1.—The Food of the Musk Turtle in Natural Waters in Michigan.

Based on seventy-three stomachs containing 17.7 cc. of food and on sixty-six colons containing 51.4 cc. of food, from 105 turtles, collected on thirteen lakes and three non-trout streams. Eight specimens from fish hatcheries not included.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Game and pan fishes	6.2	0.8	1.6	1.1
Unidentified fishes			TRACES	1.6
Carion	40.1	5.8	4.9	3.2
Crayfishes	6.2	3.3	10.6	9.7
Insects	16.9	34.2	23.6	26.9
Snails and clams	23.2	28.3	34.7	24.7
Cryptogams and Phanerogams	3.4	15.0	7.7	14.0
Vegetable debris	4.0	12.5	16.7	18.8

of parasites of fish and other animals, and possibly from its dissemination of undigested, viable seeds of aquatic plants.

CHELYDRA SERPENTINA (Linnaeus)—Snapping Turtle, Common Snapper

Range and Size.—In Michigan the snapping turtle probably occurs in every county (Fig. 2) but is most common to the south. It attains the greatest size of any of the turtles of the state. The average carapace length of 204 of the individuals trapped is 238 mm. (9.4 inches) ranging from 51 to 373 mm. The largest specimen weighed thirty pounds. Snapping turtles up to seventy



Fig. 2. Types and locations of waters from which snapping turtles were studied and general range of the species in the United States.

pounds in weight are reported by turtle trappers. Abbott (1884) saw a specimen in New Jersey that weighed sixty pounds and reports having been told of heavier ones.

Habitat and Habits.—Published observations on the habitat of the snapper show that even very small bodies of water are inhabited by this species. In New York, near Newburgh, I took a large adult from an isolated residual pool in a small stream. W. S. Blatchley (1891) found five individuals in a similar, though smaller, "mud-hole" in Indiana. Specimens in Michigan have been collected in streams, rivers, pools, ponds, and lakes of great variety and even at a distance from water. Those waters which yielded greatest returns per unit of effort expended in obtaining snappers from them were: soft-bottomed lakes and ponds in the southern half of the Lower Peninsula; lagoon-like sections of larger rivers such as the St. Joseph near Three Rivers and the Muskegon about seven miles east of the city of Muskegon; and river-mouth lakes such as White and Muskegon Lakes.

Faced with a potential enemy on land, a turtle of this species does not ordinarily retreat within its shell or move in the opposite direction as do other Michigan turtles, but at once faces-off and may even move to the attack. In the water it is more gentle; I once saw a professional turtle hunter, with bare feet and legs, enter a small live-pen crowded with sizeable snappers and worm his feet among the animals to obtain a footing on the bottom. He stood unharmed in this pen for twenty minutes while handling thirty-seven snappers one by one for examination. This species in water tends to flee the observer or collector.

The snapper is well defended by its strong jaws, which close with remarkable speed, and protected by its heavy carapace. The common name "moss-back" refers to the luxuriant, obliterative mat of firmly attached algae, predominantly *Basiacladia*, that flourishes on the backs and on the upper parts of the tails of many individuals. The turtles are thus concealed from their enemies and their chance of capturing prey is increased.

I have collected specimens during the months of April through September, inclusive; but there are occasional records of capture for other months. Individuals are not infrequently seen moving about under the ice. Evermann and Clark (1920) recorded having seen a large specimen just under the ice in Lost Lake, Indiana, on December 18, 1900; it appeared to be too much benumbed to move away even when a hole was chopped through the ice to effect its capture. Emil Krasny, of Whitmore Lake, Washtenaw County, reported obtaining a twenty-pound individual in a like manner from Whitmore Lake early in the winter of 1937-38 just after the first freeze, while the ice was yet clear. On January 26, 1938, the Michigan Department of Conservation Official News Bulletin reported a specimen having been taken under the ice in a muskrat trap in Evans Lake, Lenawee County. Kilham (1929) found a small torpid specimen in the mud of an estuary in the Charles River at Cambridge, Massachusetts, during a February thaw. In spite of the occasional discovery of snapping turtles active during the winter months, it appears that this turtle generally hibernates, from early fall (October) to early spring (March).

Hibernating snapping turtles are usually to be found in the bottom of waterways, sometimes singly and at other times in large aggregations in selected spots such as muskrat burrows, the mouths of tributary streams, in spring inlets, and under logs and banks. Some turtle hunters make large hauls from hibernating concentrations. Earl Bixby, of Berrien Springs, took five hundred pounds of snappers in the early spring of 1937 from a small channel between two of the Grand Marais Lakes just west of Stevensville, Berrien County. These turtles were buried under from one to two feet of the soft bottom material in this channel and were located and hauled out by means of an iron rod with a hook at one end. Hibernation in similar sites has been reported by Abbott (1884), Newman (1906), Clark and Southall (1920), Cahn (1937), Conant (1938), and others.

During warm seasons, the snapping turtle is found in shallow water, beside logs, stumps, or hummocks, at times lying partly buried in the mud. The depth of water selected is usually not greater than the length of the head and neck extended, for turtles lying in this manner run the head to the surface at intervals in order to breathe. It is not given to basking in the sun on logs. Presumably by retaining an extra amount of air in the lungs snappers are able to float, motionless, at the surface of the water with the eyes and nostrils just exposed. In this position they are often shot at by irresponsible persons, an important consideration if conservation of the species is deemed wise.

Food and Feeding Habits.—Snapping turtles do not ordinarily swallow food out of water. In the reptile pit at the Museums at Ann Arbor, ground beef repeatedly placed beside the pool of water was taken into the pool by snappers before it was swallowed. I have suspended a freshly killed carp (*Cyprinus carpio*) out of water in a turtle trap and have watched captive snappers come up and secure a mouthful at a time and retire under water to swallow the morsel. One snapper repeated such feeding seven times in twenty minutes, until the supply had been exhausted. Since terrestrial organisms, plant and animal, are sometimes found in the food of *Chelydra* it is probable that feeding out of water is possible.

In trapping snappers, fresh bait gave the best catches. This was contrary to reports, and a series of simple experiments was drawn up to learn how freshness determined palatability for this species. These experiments, executed by R. M. Stow under the supervision of M. D. Pirnie, were conducted in an aquarium at the W. K. Kellogg Bird Sanctuary in mid-summer. Three adult specimens, 8.1, 10.2, and 10.9 inches long respectively, were placed in a tank about three by four feet with water about two feet deep, and kept without food for six days. A small amount of chicken entrails, kept at room temperature, was offered to the turtles each day until the day on which all three refused to eat. All three turtles ate the allotment of entrails on the first three days of the experiment. On the fourth day, the small one refused to take the food, but the medium-sized turtle ate it. The largest turtle refused the morsel offered it on the fifth day, as did the smallest. On this day, the medium-sized turtle was offered two bits of food; one of which floated while the other sank to the

bottom. That which sank was taken first; the floating piece later. On the sixth day all three turtles refused to take the offerings of entrails, which by this time were exceedingly foul.

Similar tests were repeated using dead fish kept at room temperature as food, and employing the medium-sized individual as the subject. This turtle, after being without food for five days, took the fish offered for the first five days of the experiment and then refused to feed on the sixth and seventh days. By the sixth day the fish was in advanced stages of decay.

On another occasion a decaying piece of a fish that had been dead for four days was offered the 10.2-inch snapper. Immediately after the turtle had begun to eat, a piece of freshly killed fish was introduced into the opposite side of the tank. In less than a minute the turtle left the decomposing fish and went to the fresh fish and ate it. He then returned to the putrifying fish but ate no more of it; he poked it around for some time with his snout and then left it. These experiments tend to refute the common belief that the more foul the food, the more tempting it is to the snapper.

Snapping turtles feed in three distinctive ways: (1) small prey is sucked with a sudden gulp (Conant, 1938: 127); (2) large animals are seized by the jaws and held till dead, or nearly dead, and are then torn into pieces by combined action of the jaws and front feet; and (3) vegetable matter and soft-bodied animals are bitten into sections and swallowed. It is of interest that in attacking a plant stem or leaf or other resting object, the snapper uses the same swift movement of the head and jaws as when a moving animal is seized. These turtles are bottom, mid-water, and surface feeders. Fish eggs and crayfishes are taken from the bottom. Fishes of several kinds and some plants are taken from mid-water. Algae, pond lily leaves, snails, and some insects are taken from the surface.

During bottom feeding activities, snappers often root about the large rhizomes of *Nuphar advena* and frequently break off sizeable sections, which come to the surface and are taken by professional trappers as a sign that snappers are present. Snapping turtles also "roll" the vegetation during foraging activities. This "rolling" is particularly evident in beds of *Chara* where sizeable areas of the bottom may be cleared and the vegetation moved off to one side, usually toward the shore.

Bird remains have been found in snappers by Hay (1892) and by Sontag (1924). Newman (1906) saw young ducks eaten and Hurter (1911) gives a similar record. Bralliar (1922) observed the capture of a young trumpeter swan and Buckle (1925), a hawk. Abbott (1884) saw a muskrat dragged down under water. Crayfish have been found in snappers by Hay (1892) and by Paul L. Errington (unpublished notes), and snails are reported by Evermann and Clark (1920). Hatt (1932) came upon a specimen feeding on a dead green heron and Conant (unpublished notes), on one eating a dead snake. Conant also writes me that he has seen a snapper eat a freshly caught fish. Errington has written that specimens from Iowa examined by him also contained terrestrial and aquatic beetles, frogs, and vegetable matter.

The only previous detailed study of the food of the snapping turtle is that of Surface (1908) based on nineteen specimens containing food. The stomachs of five of these turtles contained plants: algae, apple seeds, leaves of skunk cabbage (*Symplocarpus foetida*), grass, and undetermined seeds and leaves. All nineteen had eaten animal matter. Snails and slugs were present in seven. Insects, found in nine, included bugs of the families Corixidae and Pentatomidae, fly larvae including Stratiomyidae, and beetles including members of the families Hydrophilidae, Dytiscidae, and Gyrinidae. Vertebrate remains, recognized in seven individuals, were fishes (suckers of the family Catostomidae among them), and frogs, snakes, birds, and mammals (mice and remains of a rabbit).

That the snapping turtle is not wholly carnivorous but rather omnivorous was early suggested by Hay (1887) and substantiated by Surface (1908). Babcock (1916) also found plant material (marsh grass, *Distichlis spicata*) in a specimen. The omnivorous habits of the snapping turtle are also shown in an unpublished study made at Portage Lake, Washtenaw and Livingston counties, by Lyle S. Hubbard under the direction of Carl L. Hubbs in 1920. A large proportion of the contents of stomachs examined by Hubbard was composed of segments of water lily stems, plant food predominating over the animal matter.

In captivity, snapping turtles will eat a great variety of animal and vegetable substances. In my laboratory they have been fed on ground beef heart, dead flies and moths, crayfishes, earthworms, and fishes. In the reptile pit at the Museums, lettuce and ground beef are fed to snapping turtles.

Observations on the food of young individuals also indicate omnivorousness. Surface (1908) found young turtles feeding on insects, especially beetles, and also on small fishes, crayfish, and snails. Newman (1906) reported that they eat larvae of insects that are found by burrowing in the mud. Linsdale (1927) found cricket frog remains in a small specimen. The smallest individual (65 mm. in carapace length) examined by me was taken from the Clinton River at Drayton Plains on July 8, 1937, at 3:00 P.M. The stomach contained a small northern blacknose shiner (*Notropis h. heterolepis*), three beetle larvae, a leech, and some filamentous algae, with a trace of a crayfish and some vegetable detritus in the colon.

Snappers taken some distance from water give little or no evidence of having fed on terrestrial plants or animals. Two in my collections contained food from the aquatic habitat as follows: (1) remains of a large hydrophilid beetle and a trace of watermeal (*Wolffia*) in the stomach, with seeds of beggar tick (*Bidens*), a small amount of *Wolffia*, remains of a snail (*Lymnaea*), a beetle, and a lepidopterous larva in the colon; (2) remains of three snails (*Physa*) and a trace of filamentous algae. Conant has written me that a small specimen found dead on the road contained the remains of terrestrial Orthoptera.

The food studies of the snapping turtle here reported are based on 323 specimens with food either in the stomach, colon, or both. These turtles were

collected during the months of May through September in 1937 and in 1938 from seventy-two lakes, eleven non-trout streams, six trout streams, and eight fish cultural stations (Fig. 2). In the following report the findings for specimens from each of Wintergreen, Sherman, and East Twin Lakes are discussed separately. Additional series treated individually are those from river-mouth lakes, non-trout streams, trout streams, and fish cultural establishments. This facilitates comparison of the food habits of the snapper in different ecological situations.

Wintergreen Lake.—This body of water at the W. K. Kellogg Bird Sanctuary of Michigan State College is relatively shallow and approximately twenty acres in surface area. The bottom is chiefly marl, with smaller areas of sand and muck. Around one end there are extensive beds of *Nuphar advena* which, with narrow-leaved potamogetons, dominates the aquatic flora.

Both game and forage fish are numerous in the lake. The most abundant sport fish is the common bluegill. Yellow perch, largemouth bass, pumpkinseed, bluegill \times pumpkinseed hybrids, yellow bullhead (*Ameiurus n. natalis*) and brown bullhead (*Ameiurus n. nebulosus*) are also present in some numbers. Forage fishes include four species of minnows, chubsuckers (*Erimyzon*) and the Iowa darter (*Poeciliichthys exilis*). The bowfin also occurs.

The twenty-one snapping turtles from Wintergreen Lake afford information on the vulnerability of waterfowl to snapping turtle predation. This is the only lake from which snappers were taken when broods of ducklings, goslings, and cygnets were *known* to have been present. According to Pirnie (1935), approximately twenty pairs of mallards nest about the lake and swale each year; some Canada geese and mute swans also nest here; adult waterfowl of several species are always present. Inasmuch as snapping turtles have been trapped or shot on this lake since 1927, a surprisingly high number was taken during the summers of 1936 through 1938. In mid-July, 1936, nine individuals averaging about ten inches in length were trapped in two nights. From June 26 through September 4, 1937, the catch for 496 trap-nights was eighteen specimens. From July 5 through August 13, 1938, the take on 153 trap-nights was eight snappers averaging about nine inches in length. Although trapping operations reduce the snapping turtle population in the lake, it seems impossible to eliminate the species entirely.

The food studies of snapping turtles from Wintergreen Lake are based on twenty-one specimens containing food (Table 2). Game fishes eaten were mostly centrarchids. Remains in the colons could not be positively identified as carrion or otherwise. Bluegills and a largemouth bass were present; other sport species taken were yellow perch and yellow bullhead. In all, the turtles studied had accounted for less than one game fish per individual. Even with the assumption that all the game and pan fishes were alive when taken (which is doubtless not true), such a toll could hardly be a menace to the large fish population of this lake. It is possible that removal of some of these fishes from this body of water by turtles or otherwise would benefit the remaining individuals, for the fishing pressure by anglers is light.

TABLE 2.—The Food of the Snapping Turtle in Wintergreen Lake.

Based on thirteen stomachs containing 287.5 cc. of food and on seventeen colons containing 604.5 cc. of food.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Game and pan fishes	10.3	46.2	0.4	52.9
Unidentified fishes	TRACE	7.7	0.2	29.4
Waterfowl	27.5	15.4	1.0	5.9
Unidentified birds	0.7	15.4	3.4	29.4
Muskrat	5.6	5.9
Carriion	5.3	7.7	0.3	11.8
Crustaceans	0.4	30.8	0.1	23.5
Water mites	TRACES	23.1	TRACES	47.1
Insects	0.6	46.2	1.1	88.2
Molluscs	1.7	30.8	0.5	47.1
Cryptogams	49.3	62.5	70.3	88.2
Phanerogams	0.3	38.5	1.8	70.6
Vegetable debris	3.9	38.5	15.4	64.7

Four young mallards were present in three turtles, but it could not be ascertained whether any of the birds were alive and healthy when taken. Director Pirnie, of the Sanctuary, has told me that in his seven summers on the grounds he has never seen, nor have any of his men seen, a bird actually being taken by a snapper. Ducklings have, however, disappeared for undiscovered reasons. In spite of the high concentration and availability of avian prey, it appears that the snapping turtles on this lake turn largely to the still more available aquatic vegetation for food. The turtles certainly cannot be blamed for the entire amount of loss of young waterfowl. There is evidence that largemouth bass, other predacious fishes, and bullfrogs take ducklings.

Feathers alone constituted the unidentified bird remains in one stomach and in two colons. These feathers may have been taken from the water's surface or from the bottom of the lake, or they may represent a bird that escaped from the turtle's attack. No bones or flesh were present with these feathers. Remains of other unidentified birds were found in four additional turtles. The remains of a starling in one individual were classed as carrion since several had been shot near the lake on the day previous to the capture of the turtle.

In Wintergreen Lake, as in many other lakes, the food most available to turtles is aquatic vegetation and this material is by far the most important by bulk and by frequency of occurrence in both stomachs and colons of the individuals studied. Filamentous algae, almost always present in quantities either on the surface or on the bottom of this lake, constituted the major portion of the vegetable matter taken. Many miscellaneous invertebrates, which make up but a small proportion of the total volume but which are always associated with these plants and so have a high frequency of occurrence, were perhaps secondarily ingested with the algae.

Sherman Lake.—This lake is briefly described above (p. 261).

Nineteen common snappers containing food were studied from this body of water. Seventeen of these were collected on August 19-21, 1937, and two on September 16-17, 1938. The average size of eighteen of these specimens was 274 mm. (10.8 inches), ranging from 208 to 305 mm.

Game and pan fishes taken by snappers from Sherman Lake, as for the other lakes studied, were predominantly centrarchids; bullheads and yellow perch were also represented. Fishes in the stomachs were clearly alive when taken; the scanty remains found in the colons could have been carrion. At the most, however, the turtles averaged less than one and one-fourth such fishes per individual, during the time of feeding represented by the stomach and colon contents.

Aquatic vegetation is the predominant food in stomachs and colons and occurs in all colons that contained food remains (18) and in all but one stomach that contained food (14). Filamentous algae form the most important single item in both organs, with *Nymphaea odorata* next. In addition to the quantities of leaves and petioles of *Nymphaea* present in four stomachs and five colons, one of these stomachs and the colon of the same individual contained 11,065 seeds (65 cc.) of this plant. The seeds were apparently mature and very few of the coats were ruptured. As in the case with the musk turtle, the snapping turtle may be a significant agent in the dispersal of the seeds of such aquatic plants.

East Twin Lake.—This lake has an estimated area of forty acres (Henshaw, 1931) and a maximum depth of forty feet. The shoreline is partly hilly and wooded and partly swampy. Bottom types are predominantly fibrous and pulpy peat and marl with a little sand at the inlet. The small outlet, Bigelow Creek, flows into Muskegon River. Several cool springs occur in the soft, peaty bottom of the north end of the lake. Shoal areas are extensive at the north and south ends of this body of water. The principal plants are filamentous algae, *Chara*, mosses, potamogetons, *Najas*, *Anacharis canadensis*, *Lemna*, *Spirodela polyrrhiza*, *Ceratophyllum demersum*, *Ranunculus*, *Myriophyllum*, *Polygonum*, *Decodon verticillatus*, *Scirpus*, and *Typha*.

Game and pan fishes collected by me from this lake are largemouth bass, northern rock bass, bluegill, pumpkinseed, yellow perch, and brown bullhead. Common white suckers (*Catostomus c. commersonnii*), several species of minnows, and Johnny darters (*Boleosoma n. nigrum*) and Iowa darters occur. Muddlers (*Cottus*) are present at the outlet.

The turtle species are the mid-western painted turtle, snapping turtle, Blanding's turtle, map turtle, and the musk turtle (listed in order of decreasing abundance). Particularly favorable to the turtle population of this lake are the facts that the lake is private and well-removed from travelled roads; that several springs in the soft bottom at one end and a tributary trout stream furnish excellent winter quarters; that extensive shoal areas provide for foraging; and that the lake is seldom fished and thus presumably has a very large fish population.

Twenty-five snappers available for food study were collected in 1938

between July 11 and 27, and on August 16 and 17. These turtles ranging from 180 to 374 mm. averaged 263.8 mm. (10.3 inches) in length.

Game and pan fishes assume a considerable importance by volume (60.9%) in the stomachs. By numbers, however, the average, including those in both the stomachs and in the colons, is less than one and a half such fish per turtle for the feeding period represented by the sample. As in other series, it was impossible to determine whether the fishes (predominantly centrarchids) present in colon contents were dead or alive when taken. The yellow perch, bluegills, and pumpkinseeds found in the stomachs were apparently alive and healthy when eaten. Aquatic plants make up the balance of the food in the stomachs and almost all of that in intestines.

River-mouth lakes. — Specimens from Muskegon and White Lakes are grouped together. These are ecologically very similar and good-sized bodies of water situated near Lake Michigan at the mouths of the two large rivers whose names they bear. They have extensive areas of marsh, and sand and silt shoals. Considerable shoreward expanses are underlain by quantities of water-logged mill waste and many "dead-heads." The mill waste, consisting of long strips of bark and wood trimmings dumped irregularly on the bottom, abounds with crevices and provides a favorable habitat for crayfish, snails, and other invertebrates, which are particularly abundant. Aquatic vegetation is plentiful in the shallower water not too much exposed to wave action.

Seven snappers from White Lake and nine from Muskegon Lake, collected in late August and September contained food in thirteen stomachs and in all colons. The average length of fourteen individuals measured is 228 mm. (9.0 inches), ranging from 144 to 321 mm.

As in Sherman Lake, the food of the snappers from these river-mouth lakes shows game and pan fishes to comprise an unusually high proportion (67.6%) of the food in stomachs. The species taken include bullheads, yellow perch, largemouth bass, bluegills, and pumpkinseeds. It was impossible to determine the origin, as carrion or otherwise, of the fishes in the colons, most of which were represented only by traces. Counting all the game fish represented in stomachs and colons the average is very little more than one per turtle. Owing to the extensive water area it is doubtful that such an incidence in the food of the snapper offers any occasion for concern to the sportsman or to commercial fisheries.

A seven-inch bluegill with a No. 6 fish-hook firmly lodged in its hyoid region was found in the stomach of a turtle 321 mm. long; the injury suffered by the bluegill may have been the direct cause of its capture.

As might be expected from their abundance in these lakes, crayfish are represented in larger proportions than anywhere else in my findings, both in stomachs (22.3% by volume, 53.8% by frequency) and colons (35.3% by volume, 100.0% by frequency). As a result of this abundance of crayfishes and of game fishes in the food, aquatic vegetation is present proportionately less, comprising the balance of the food for each set of organs. The principal

plants found were filamentous algae and the duckweeds, *Lemna trisulca* and *Spirodela polyrhiza*.

Non-trout streams.—Nineteen turtles containing food were collected during summer months from eleven non-trout streams. Eleven of these specimens ranged from 65 to 317 mm. and averaged 218 mm. (8.6 inches) in length.

The entire volume (19.3%) of game and pan fishes in the stomachs was made up by a yellow perch and a smallmouth bass in one turtle. Including all such fish present, even those in the colons which occurred as traces and may have been carrion when taken, only about one out of every three turtles showed evidence of having eaten game species. Fish recognizable as carrion were a rock bass and a bluegill. In this series crayfish are of proportionately greater importance, which may be due to a generally greater abundance per unit area in stream than in lake habitats, excepting such river-mouth lakes as previously cited.

Trout streams.—Only six specimens were secured from waters of this ecological type during the summer months. The snapping turtle population is doubtless lower in such streams than for warmer, non-trout streams of comparable size, and little attempt was made to secure specimens from this habitat.

The high proportion of crayfish (87.0% of the bulk in stomachs) in the food of these snappers corresponds to the fact that crayfish are probably the most readily available food in trout streams. On the basis of the numbers contained in the stomachs only, the five turtles averaged a little more than four crayfish each. In the one colon (turtle 279 mm. long) that contained crayfish, there were remains of a large, unascertained number with a volume of 450.0 cc. The nine-inch trout found in one stomach may have been taken alive or as carrion.

Fish hatcheries.—Twenty-one summer taken specimens containing food (Table 3) were available for study from eight hatcheries in the Lower Peninsula. The average size of twelve measured specimens ranging from 51 to 294 mm. is 210 mm. (8.2 inches).

Unusually large numbers of fishes are concentrated in ponds and raceways at fish hatcheries and rearing stations. Since it is generally assumed that such concentrations create an increased vulnerability of the fish to their predators, it is noteworthy that the snappers took game fishes in no greater amounts than did the turtles collected from some natural waters. The average for turtles from fish hatcheries is approximately one game fish for each three turtles. Considering the possible benefit derived from the destruction of the runts and diseased fishes and of numbers of predacious insects, the predation of snapping turtles at hatcheries under certain conditions seems to be innocuous.

Where fish are being removed from hatchery ponds by fyke nets or other means that tend to concentrate them in an enclosure also accessible to turtles, where they are extremely crowded in raceways, or where eggs of pond-fishes are placed on trays in rearing ponds, snapping turtles can not be tolerated. The limitation of production in fish cultural establishments by this species is, however, less than has been supposed.

TABLE 3.—THE FOOD OF THE SNAPPING TURTLE AT FISH HATCHERIES.

Based on eighteen stomach containing 1,049.3 cc. of food and on ten colons containing 336.7 cc. of food.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Game and pan fishes	54.5	27.8	1.1	10.0
Forage fishes	26.9	16.7	0.4	30.0
Unidentified fishes	3.9	22.2	0.3	20.0
Frogs and toads	1.2	16.7	0.5	40.0
Crayfishes	8.0	61.1	41.6	80.0
Insects	1.0	38.9	1.9	80.0
Miscellaneous animals *	0.4	5.6	0.4	40.0
Cryptogams	2.1	27.8	6.1	40.0
Phanerogams	0.4	27.8	10.6	40.0
Vegetable debris	1.6	16.7	37.1	70.0

* Includes remains of a meadow mouse and a muskrat in one stomach and water mites and a scud in one colon and snails in four colons.

ANNOTATED LIST OF ITEMS IN THE FOOD OF 323 SNAPPING TURTLES

In the following list the numbers of specimens of each food item as determined by actual count (when feasible) are given with detailed identifications of the substances taken. It was sometimes impracticable or impossible to determine the number of individuals composing some of the food items, in which case notes on relative abundance are entered. Excepting seeds, plant materials are of necessity recorded in this fashion.

Game and pan fishes.—Of two trout found in stomachs, one was identifiable as the eastern brook trout (*Salvelinus f. fontinalis*). Fourteen bullheads included 5 northern brown bullheads and 3 northern yellow bullheads. In the pike family, 6 individuals could be recognized of which 4 were mud pickerel (*Esox vermiculatus*) and 1, a northern pike. Eighteen yellow perch occurred. The sunfish family was represented by 264 individuals distributed as follows: northern smallmouth bass, 5; largemouth bass, 6; common bluegills, 43; pumpkinseeds, 45; northern rock bass, 1; and miscellaneous centrarchids, 164. Of the game and pan fishes previously enumerated, the brook trout, 3 smallmouth bass, 2 largemouth bass, 13 bluegills, and 28 pumpkinseeds had been eaten at the fish hatcheries.

Forage fishes.—Six suckers were recognized. Of 33 minnows, 17 were western golden shiners (*Notemigonus crysoleucas auratus*), 1, a common shiner (*Notropis cornutus*), and 1, a northern blacknose shiner. Eight mudminnows (*Umbra limi*), 2 Johnny darters (*Boleosoma nigrum*), 2 Iowa darters, and 1 fantail (*Catnotus f. flabellaris*) complete the list. Of these, 1 sucker, 14 golden shiners, 1 common shiner, and 5 other cyprinids were contained in snappers collected at fish hatcheries.

Fish eggs.—A large number (20,520) of eggs, presumably bluegill, were found in the stomachs of three snapping turtles.

Other vertebrates.—Vertebrates other than fishes were: mudpuppy (*Necturus maculosus*), 1; American toad (*Bufo americanus*), 1; bullfrog (*Rana catesbeiana*), 3; pickerel frog (*Rana palustris*), 1; unidentified frogs or toads, 11; musk turtles, 10; common snapper, 1; Blanding's turtle, 1; common mallard (*Anas p. platyrhynchos*), 1; blue-winged teal (*Querquedula discors*), 1; Florida gallinule (*Gallinula chloropus*), 1; unidentified birds, 4; muskrat (*Ondatra zibethica*), 2; eastern meadow mouse (*Microtus p. pennsylvanicus*), 1.

Carion.—The following animal species were identified as carion and therefore have not been given elsewhere in this list: bluntnose minnow, yellow perch, largemouth bass, northern rock bass, common bluegill, black crappie (*Pomoxis nigro-maculatus*), exuvium of the blue racer (*Coluber constrictor flaviventris*), musk turtle, and European starling (*Sturnus v. vulgaris*).

Miscellaneous invertebrates.—Freshwater sponge material, an earthworm, a tubificid, and four leeches were in stomach contents.

Crustaceans.—Several scuds (*Hyaella knickerbockeri*) and other amphipods were found. Crayfishes (*Cambarus*) not identified to species numbered 146; others were: *C. virilis*, 127; *C. immunis*, 21; *C. propinquus*, several; *C. robustus*, 1; and *C. diogenes*, 6.

Water mites.—Several species of water mites were present as follows: *Diplodontus despicens*, few; *Limnesia undulata*, 2; *Unionicola crassipes*, 1; *Neumania ovata*, 1; *Neumania armata*, 3; *Neumania semicircularis*, few; *Neumania* sp., 1; *Koenikea wolcotti*, 1; *Forelia liliacea*, 1; *Piona reighardi*, 2; *Piona pugilis*, 5; *Piona wolcotti*, 1; *Piona* sp., 2; *Mideopsis orbicularis*, 1; *Arrenurus infundibularis*, 2; *Arrenurus manubriator*, 1; *Arrenurus marshallae*, 5; *Arrenurus megalurus*, few; *Arrenurus megalurus intermedius*, 2; *Arrenurus wardi*, 2; *Arrenurus falcicornis*, 2; *Arrenurus* sp., 27.

Insects.—Insects of the following groups were present: *Orthoptera*, 1; *Corydalis* larva, 1; *Ephemerella bicolor* nymphs; *Caenis* nymphs; *Ephemeroptera* nymphs; *Anax junius* nymph, 1; *Libellula* nymph, 1; *Leucorrhinia* nymph, 1; other anisopteran nymphs; *Enallagma* nymphs, 3; other zygopteran nymphs; miscellaneous odonate nymphs, 4; *Corixidae*, 5; *Plea striola*, 1; *Ranatra*, 2; *Lethocerus*, 6; *Benacus*, 2; *Belostoma*, 10; *Belostomatidae*, 12; *Gerridae*; other *Hemiptera*, 1; *Homoptera*, 1; *Haliphus*; *Peltodytes* larvae; *Haliplidae*, 2; *Acilius*, 1; *Dytiscidae*, 90; *Gyrinidae*, 4; hydrophilid larvae and adults, 32; *Elmidae*, 1; *Chrysomelidae*, 2; *Curculionidae*, 1; other beetle larvae and adults; hydroptilid larvae, 11; larvae of *Phryganea*; leptocerid larvae; other trichopterous larvae; *Tipulidae*, 8; chironomid larvae and pupae; ceratopogonid larvae; larvae of *Stratiomyia*, 1; several unidentifiable insects.

Snails and clams.—Identified were: *Lymnaea emarginata*; *Lymnaea* sp.; *Helisoma trivolvis*; *Helisoma antrosom*; *Helisoma campanulatum*; *Helisoma* sp.; *Gyraulus parvus*; *Gyraulus hirsutus*; *Gyraulus* sp.; *Planorbula armigera*; *Planorbula* sp.; *Physa sayii*; *Physa elliptica*; *Physa* sp; *Campeloma* sp.; *Valvata*

tricarinata; *Valvata sincera*, 10; *Bithynia tentaculata*, 116; *Amnicola limosa*; *Amnicola integra*; *Amnicola lustrica*; *Amnicola* sp.; *Sphaerium striatinum*; *Sphaerium* sp.; *Pisidium abditum*; *Pisidium* sp.

Cryptogams.—In addition to a small amount of moss the following algae were found: *Oscillatoria princeps*; *Oscillatoria* sp.; *Lyngbya*; *Anabaena*; *Nostoc*; *Tolypothrix*; *Ulothrix*; *Coleochaete nitellarum*; *Cladophora glomerata*; *Cladophora* sp.; *Rhizoclonium hieroglyphicum*; *Rhizoclonium* sp.; *Pithophora varia*; *Oedogonium*; *Hydrodictyon reticulatum*; *Vaucheria*; *Mougeotia*; *Zygnema*; *Scenedesmus scutiformis*; *Spirogyra crassa*; *Spirogyra* sp.; *Chara*; *Nitella*.

Phanerogams.—Flowering plants represented were: *Typha*; *Potamogeton*; *Najas*; *Anacharis canadensis*; *Vallisneria spiralis*; various Gramineae; *Phragmites communis*; *Scirpus*; *Peltandra virginica*; *Spirodela polyrhiza*; *Lemna trisulca*; *Lemna minor*; *Lemna* sp.; *Wolffia*; Lemnaceae; *Salix*; *Ceratophyllum demersum*; *Nuphar advena*; *Nymphaea odorata*; Nymphaeaceae; *Brasenia Schreberi*; *Ranunculus*; Rosaceae; *Acer*; *Myriophyllum*; *Cornus Amomum*; *Cornus* sp.; *Utricularia*; Compositae; *Bidens*; *Lycopersicon esculentum*.

SUMMARY AND CONCLUSIONS

A summary of the food contained in 173 stomachs and 261 colons of 281 snapping turtles collected from natural waters is given in Table 4. The volumetric relationships of items in the stomachs are shown in Fig. 7. The data for the twenty-one specimens from Wintergreen Lake are not included since this lake is abnormal in its unusually high waterfowl population. The twenty-one specimens from fish hatcheries are also omitted.

Considering only the stomach contents, game and pan fishes, carrion and plants appear as the most important foods of this turtle. On the basis of stomach contents about one-third of the food of the snapping turtle in Michigan is composed of game and pan fish. Another third is composed of vegetable matter, almost entirely the leaves and petioles of aquatic plants, eaten by three out of every four individuals. The remaining third is largely the remains of

TABLE 4.—The Food of the Snapping Turtle in Natural Waters in Michigan.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Game and pan fishes	34.2	32.4	2.1	51.7
Forage fishes	0.3	5.8	0.4	10.3
Unidentified fishes	0.9	12.7	2.1	35.2
Other vertebrates	1.1	2.3	1.1	7.2
Carrion	19.6	6.4	1.3	2.7
Invertebrates	7.8	49.7	23.9	82.4
Vegetable matter	36.2	74.6	69.2	93.5

dead animals but includes significant quantities of crayfish, snails, and insects.

If one regards the results of the analyses of colon contents only, about one-fourth of the food appears to be composed of invertebrates, principally crayfish, and three-fourths to be composed of aquatic vegetation.

If the remains of all the game and pan fishes found in the food of the snappers studied from wild waters were of fishes that were alive and healthy when taken, 302 turtles would have accounted for 275 live fishes, over the period of time represented by the remains in the digestive tract. Since this figure must be considerably reduced by the proportion of specimens taken as carrion the minimal significance of this species to game and pan fish populations seems apparent. It seems a conservative estimate that on the average not more than one game or pan fish is eaten per day by the individual snapping turtle.

To interpret in another way the data on numbers of game fish eaten by snapping turtles in natural waters, still assuming all fish encountered to have been alive and healthy when taken, the 186 stomachs that contained food averaged approximately five-tenths of a game and pan fish each, whereas the 278 colons with food averaged seven-tenths of such a fish each. Recalling that the contents of each stomach probably represented a partial "meal," and that each colon probably includes the remains of several feedings, we may assume that the contents of 186 stomachs and 278 colons (of 302 specimens from natural waters) approximately represent 454 sample "meals." In this large number of meals, the creel fish average six-tenths of an individual per turtle. This interpretation probably offers the truest picture of predation on game fishes by snapping turtles.

Most game and pan fishes eaten by the snappers were less than legal size, and such smaller fishes are much more abundant in nature than those of legal size. Populations of snappers were estimated by the mark and recapture method in Wolf and East Twin Lakes to approximate two snapping turtles per acre of surface area in these waters. These considerations further minimize the significance of the estimate that each snapper on the average consumes six-tenths of a game fish per feeding. Thus there need be little concern as to the adverse relations of snapping turtles to game fish populations in wild waters.

Since forage fishes are more often abundant in waters than are game fishes, it is surprising to note their fewness in the food of the snappers studied. They averaged about one to every ten of the 462 sample meals. Consequently, this turtle does not appear to have a significant role in the current decline of forage fish populations, nor does it seem to compete significantly with game fishes for this type of food.

It is regrettable that more complete information is not available on the relations of this turtle to nesting game and pan fishes, but too few specimens were obtained from the vicinity of spawning beds to afford conclusive data in this respect.

No vertebrates other than fishes were found in sufficient numbers to warrant recommendations that populations of this turtle be reduced. Attack on waterfowl, young or adult, is hardly more than suggested. Despite the local concen-

tration of waterfowl the series of twenty-one specimens from the W. K. Kellogg Bird Sanctuary contained the remains of only four young mallards in a total of some thirty "meals." Recalling that it could not be ascertained whether or not these birds were alive and healthy when taken, the somewhat damaging nature of this evidence is reduced. In 434 meals in natural waters (not including sanctuary and fish hatchery waters), feathers were found three times and remains of a Florida gallinule and a blue-winged teal once each. Contrary to report, there is an extremely low incidence of bird remains in the food of the snapping turtle.

Crayfishes include the greatest number of invertebrates taken. Insects, mollusks, water mites, and a miscellany of other invertebrates, although occurring in large numbers, account for a relatively insignificant proportion of the total food volume. The greatest significance of the feeding habits of the snapping turtle to game and pan fishes may be the competition which they offer for such food, since fishes forage upon many of the same organisms.

The consumption of mollusks by this turtle may be of importance in interrupting the life cycles of certain parasites and thus may have an indirect economic significance.

Vegetable matter is clearly the principal food substance. The extent to which feeding upon aquatic vegetation by snappers may be regarded as harmful or beneficial requires separate consideration for each body of water. As pointed out by Hubbs and Eschmeyer (1938), it may be desirable to control aquatic plants in some circumstances and to encourage their growth in others. Obviously this turtle has some habits that tend to crop and others that may disturb water plants. Other habits may spread them. Plants are cropped by being fed upon and are uprooted by snappers while foraging for other organisms. Spread of aquatic plants is doubtless accomplished by the passage of undigested seeds with feces. Where large amounts of plant materials are eaten, fewer fish and fish-food organisms find their way into the diet of this turtle, so that the effect of feeding on plants may be beneficial to the game and pan fish population.

The considerable importance of carrion in the food of the snapping turtle is suggestive of a desirable service rendered to man by this turtle. Doubtless the snappers eat many dead and dying fishes and other matter that might otherwise form obnoxious litter on resort beaches and elsewhere.

Much time in the field was spent in studying the importance of the snapper fishery for the market (See Clark and Southall, 1920). During the summers of 1937 to 1939 the market demand far exceeded the supply. Trappers found a ready sale for all the turtles caught at wholesale prices ranging from five to eight cents per pound, live weight. These trappers have mobile units and obtain snappers mostly by means of traps made of seine twine on wire hoops with a single funnel-shaped opening (Lagler, 1943). Captured turtles are held and fed in a live-pen until several hundred pounds have accumulated. They are then shipped alive in a barrel or crate to market. The best markets for Michigan turtles are in Chicago and various cities in northern Indiana and Ohio. The greatest demand comes from the restaurant trade, but many turtles are sold to

private individuals. Retail prices range from ten to twenty cents per pound liveweight and twenty to thirty cents dressed.

A trapper and helper operating about five dozen traps in Michigan waters report an average profit of a thousand dollars for each of the last three summers. Others state that revenue derived from this occupation has enabled them to make a living during recent years of economic depression.

The food habits data here presented give some indication of harmful effects of snapping turtles in aquatic communities. Considering also the services rendered to man, it seems best to recommend their conservation, except in waters where special investigation proves them to be undesirable. Conservation measures would help to ensure a sustained yield of these reptiles to professional trappers. The imposition of restrictions on turtle hunters as to minimum sizes to be taken and mesh-size to be used in traps might be desirable. Six inches, measured lengthwise and horizontally through the carapace, should be fixed as the minimum size for this purpose. A three-inch square mesh in traps would almost automatically establish this limit. An eight-inch turtle is about the smallest which has any real market value, although smaller sizes are often taken indiscriminately and shipped. The length-weight relationship in the snapping turtle, useful in determining regulatory measures, is given in another report (Lagler and Applegate, MS).

CLEMMYS GUTTATA (Schneider)—Spotted Turtle

Range and Size.—The spotted turtle is uncommon in Michigan and is not recorded from the northern half of the Lower Peninsula; the most northerly record is from Lake County. The species averages less than 127 mm. (5.0 inches) in carapace length.

Habitat and Habits.—Many authors consider this small turtle to be essentially aquatic, inhabiting small waters. A few suggest that it may have terrestrial habits at certain seasons of the year (in addition to the time of egg-laying). The spotted turtle is given to basking in the sun on objects out of the water, as are the map, painted, and Blanding's turtles.

Extensive field work in the normal haunts of the painted, Blanding's, musk, and snapping turtles failed to yield any specimens of *Clemmys guttata*. It therefore seems logical to assume that the species may be common only in restricted localities within its range in Michigan.

Food and Feeding Habits.—Excepting the work of Surface (1908), no extensive studies of the food of this species appear in the literature. Summarizing the findings of earlier workers, however, one discovers the following items reported as food of spotted turtles: frogs, tadpoles, insects and their nymphs and larvae, earthworms, mollusks, crickets, grasshoppers, plant stems and leaves, dead fish, and birds.

Surface (1908) studied the contents of twenty-seven stomachs of this species and found: vegetable matter in 3; annelid worms in 1; mollusks in 3; crustaceans in 8; myriapods in 1; spiders in 2; and insects (principally Coleop-

tera, Odonata, and Diptera) in all 27. Of interest is the fact that Surface encountered no vertebrates in the food of this turtle.

SUMMARY AND CONCLUSIONS

It seems rather clear, from the food and habitat preferences stated by other workers, and because of its uncommon occurrence, that the spotted turtle can be of no economic concern, especially in fish management, in Michigan.

CLEMMYS INSCULPTA (Le Conte)—Wood Turtle

Range.—The wood turtle was not known from Michigan prior to 1915 (Thompson, 1915a). Since that time it has been recorded from several counties in the northern two-thirds of the Lower Peninsula and in the Upper Peninsula. It remains unknown from the three southern tiers of counties across the state, and from the "Thumb" (Fig. 3). The species in Michigan averages between 178 and 279 mm. (7-11 inches) in carapace length.

Habitat and Habits.—Accounts of the habitat of the wood turtle indicate that the species occurs on land for most of its activities excepting mating or hibernation. The best accounts of the natural history of this species are those of Wright (1918) and Babcock (1919).

Food and Feeding Habits.—Many workers have published notes on the food and feeding habits of this species. Verrill (1863: 196) reported discovering specimens feeding on the leaves and scapes of dandelions (*Taraxacum densleonis*). Smith (1883: 659) observed that they feed on low field blackberry and other vegetables. Allard (1909: 453) watched a specimen feed greedily on mullein leaves (*Verbascum thapsus*), common sorrel (*Rumex acetosella*), and strawberries. Netting (1936) also found a specimen eating strawberries. Babcock (1919: 406) states that the species is omnivorous, but shows a distinct partiality for vegetable food, especially berries. Morgan (1930: 402) likened the terrestrial feeding habits of the spotted turtle to ground-feeding birds: blackberries, partridge berries, and mushrooms. She noted, however, that in water they live on a diet of small aquatic animals. Surface (1908: 162-163) has made the only detailed study of the food of this species. He found that 76 percent of twenty-six specimens that contained food had eaten vegetable matter whereas 80 percent had eaten animal matter. Among those that had eaten animal tissue seven had taken mollusks, and fourteen had eaten insects.

Netting (1927: 4) offered an explanation of the incidence of bird remains in the specimens studied by Surface (*loc. cit.*). He wrote:

The Wood Turtle (*Clemmys insculptus*) is so largely herbivorous and so mild tempered that it seems unlikely that it ever drags down and eats living birds. The bird remains which Surface reports (1908: 192) from the stomach contents of this species may have been those of a bird which the turtle had found floating dead on the water. Furthermore, after the spring mating season the Wood Turtle is largely terrestrial.

The habitat preferences of the wood turtle, its food habits, and its relative scarcity in Michigan, all have indicated that the species can have little signifi-

cance from the viewpoint of fish management. Consequently no special effort was made to obtain specimens.

Food in the digestive tracts of nine adult specimens collected in Michigan (Fig. 3) was as follows:

- (1) 2.8 cc. of filamentous algae and willow leaves (*Salix*).
- (2) 11.0 cc. of plant material (mostly algae) and insect remains including 3 blackfly larvae.
- (3) 60.0 cc. of filamentous algae including several caddis larvae (Trichoptera) and many small mollusks.
- (4) 10.6 cc. of remains of a beetle, a tadpole (*Rana*), and a snail (*Helisoma*).
- (5) 37.5 cc. of a bluegill and 46.5 cc. of larvae of caddisflies (Limnephilidae) and their houses.
- (6) 2.4 cc. of food remains including 14 *Brachycentrus* larvae, 2 limnephilid larvae, 1 neuropteran larva, a snail, and a leaf fragment.
- (7) 2.1 cc. of limnephilid larvae (6) and their houses and a trace of a leaf.
- (8) 4.8 cc. composed of 5 oligochaete earthworms, 1 adult of Hymenoptera, moss, willow leaves, leaves of grass, and vegetable debris.
- (9) 1.8 cc. comprised by remains of 1 trout (Salmonidae), insects, and vegetable debris including some algae.

SUMMARY AND CONCLUSIONS

The analysis of the food of nine Michigan specimens confirms both the more extensive study by Surface (1908), and the natural expectation from its predominantly terrestrial habits, that this turtle can be of no concern to fish management.

EMYSL BLANDINGII (Holbrook)—Blanding's Turtle

Range and Size.—In the Lower Peninsula of Michigan, Blanding's turtle is known from most counties and probably occurs over all of the area. In the Upper Peninsula it has been recorded from only one locality, in Marquette County (Fig. 4).

Although individuals may attain a size of 236 mm. (9.3 inches, greatest length through the carapace of an adult male in my collections), 200 mm. (eight inches) is the average size of forty-four adult males and females selected at random from among the specimens which I studied for food. Ruthven (1927) considered 230 mm. as an unusually large size for this species in Michigan.

Habitat and Habits.—Published accounts on the habits and the habitat preferences of Blanding's turtle are few, as compared with the information on the other turtles which occur in the state. Some authors (Blanchard, 1928; Thompson, 1911; Hankinson, 1917; etc.) report finding this turtle in water;

others (Potter, 1920; Garman, 1892; Hay, 1883; etc.) report finding it on land. Schmidt and Necker (1935) state that it is abundant in sloughs during the spring and on land in the summer and fall. In my field studies of Blanding's turtle in Michigan, no attempt was made to learn of the terrestrial habits. Except for a few females taken along highways not far from water in late spring and early summer during the nesting season, all specimens of this turtle which I have observed or collected in Michigan were in aquatic habitats: lakes, ponds, creeks, rivers, and hatchery ponds. In such places they are commonly associated with musk, snapping, painted, and map turtles.

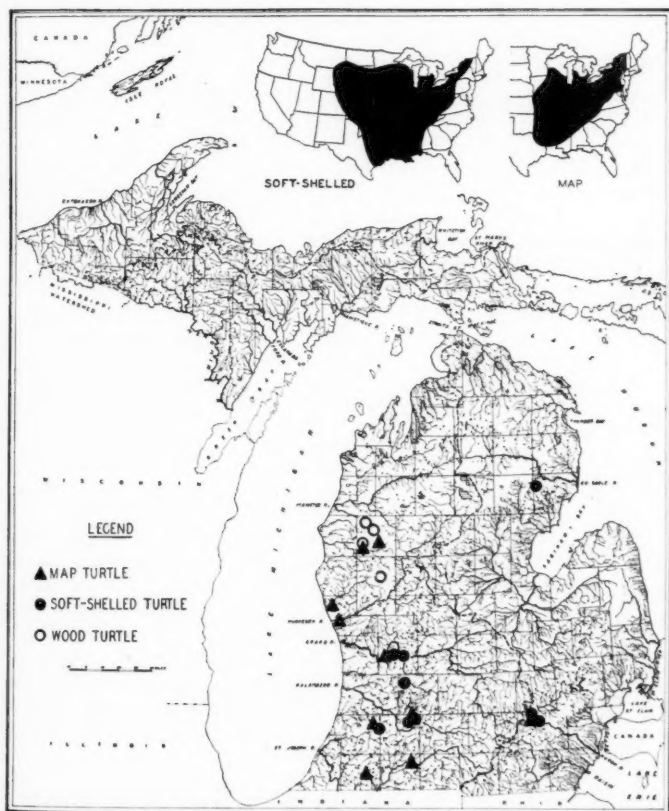


Fig. 3. Locations from which wood, map, and soft-shelled turtles were studied and range of the map and soft-shelled turtles in the United States.

Notwithstanding the restriction of my work to the habitats listed, I am inclined to feel that in Michigan, at least, this species is much more aquatic than the literature might lead one to believe. As evidence of the aquatic propensities it may be mentioned that during the months of May through September, in the summers of 1937 and 1938, forty-seven specimens were taken in turtle traps from Wolf Lake, Van Buren County, and fifty-two were collected by this means in East Twin Lake, Newaygo County. In addition, they are fairly adept swimmers and are also given to basking on objects out of, though near, the water; they retreat to the water at the slightest disturbance and usually move toward the drop-off. Conant (1938) has observed specimens moving about under the ice in captivity and hibernating in this environment but also records hibernation on land under circumstances similar to those I have observed for the snapping turtle.

Food and Feeding Habits.—Specimens in the reptile pit at the University Museums have been observed to take ground beef into the water before swallowing it. They have not been seen to swallow food out of water. Captive specimens in tanks in the laboratory have soon learned to take ground beef from the hand and have always retired under water before swallowing. Carl L. Hubbs has had live minnows captured by members of this species in small aquaria. Regarding feeding habits, specimens in a large exhibit pool at the State Fish Hatchery near Oden, Emmet County, have been seen rooting about under the detritus on the bottom of the pond in two to three feet of water. Although crayfishes and aquatic insect larvae were present in this pond, no captures of these organisms were observed. In this type of foraging activity the head was used to turn over small flat stones on the bottom and the head and claws were employed to enlarge and explore recesses under bulky objects. That they may at least sometimes feed in moderately deep water was shown by an observation of two individuals which were foraging at night on the bottom in water seven feet deep in Wolf Lake, Van Buren County.

My food studies of Blanding's turtle are based on sixty-seven specimens which contained food either in the stomachs or colon or in both. These turtles were obtained from seventeen lakes, two non-trout streams, one trout stream, and three fish hatcheries during the months of May through September mostly in 1937 and in 1938 (Fig. 4). Enough specimens with food were obtained in Robinson and East Twin Lakes to warrant a brief separate consideration of the material from each of these bodies of water. Individuals from many other lakes have been combined into one group, those from fish rearing stations into another, and those from non-trout streams into yet another. For each of these groups the findings are discussed individually. In the annotated list are given details of the numbers and kinds of the items eaten, and in Table 5, a summary of the food of this turtle for all natural habitats.

Robinson Lake.—This small, shallow lake in Newaygo County has an abundance of aquatic vegetation growing from a very soft bottom. The eleven Blanding's turtles studied for food from this water were collected on August 30, 1938. Their average length is 168 mm. (6.6 inches), ranging from 119 to

190 mm. Four stomachs contained no food but some food was present in each of the eleven colons.

In Robinson Lake, the principal foods of this turtle as seen by volume in stomachs are very definitely crayfishes (29.9%), aquatic insect larvae (35.1%), and fish carrion (24.7%). The same holds for the food as seen in the colons, except that here the remains of crayfishes (43.0%) and those of insects (51.7%) compose practically all of the food. The dead fishes eaten were of less than legal size and apparently had been returned to the water by anglers. The food of these specimens is very similar to that of two snapping turtles

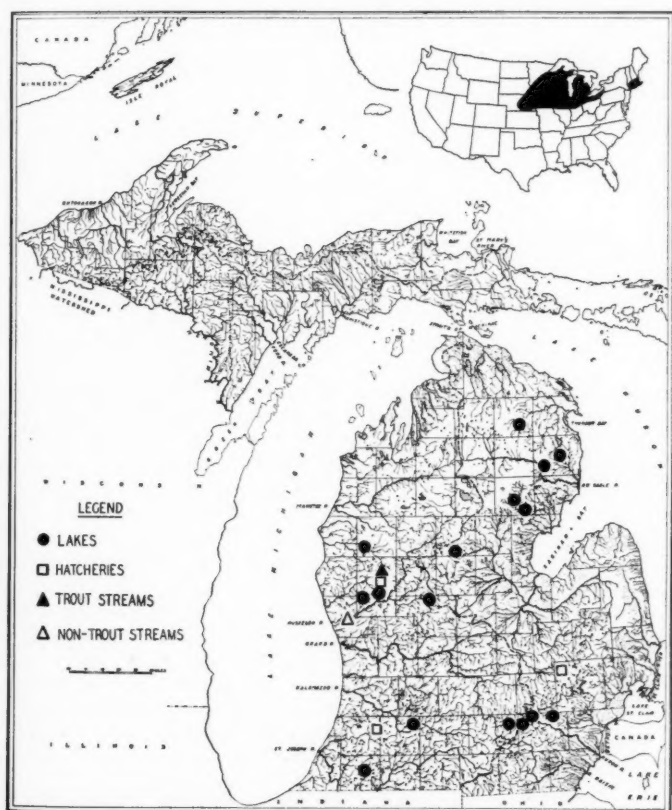


Fig. 4. Types and locations of waters from which Blanding's turtles were studied and general range of the species in the United States.

collected from this lake at the same time. The snappers, however, had eaten a little more aquatic vegetation than had the Blanding's turtles. The principal effects of the Blanding's turtles on the game fishes of this lake at this time appeared to be in competition for food.

East Twin Lake.—A brief description of the biological and physical features of East Twin Lake has previously been given (p. 272). Eleven of the Blanding's turtles which contained food for analysis from this body of water were collected on May 19-20, 1937, one on July 12-13, 1938, and another on August 16-17, 1938. These thirteen turtles averaged 212 mm. (8.3 inches) in carapace length, ranging from 181 to 236 mm. Forty-one additional individuals of the species which were trapped in this lake were measured, marked for future recognition, and released as a part of population-density and growth-rate studies.

The two principal food items by volume in the stomachs of the Blanding's turtles from this lake, as for Robinson Lake, were obviously crayfishes (52.1%) and aquatic insect larvae (41.4%). The contents of the colons by bulk was 69.3 per cent crayfish remains and 26.5 per cent insects. No carrion was found, perhaps because most of the turtles were taken before the fishing season opened and before the spawning season for centrarchids was under way. Aquatic vegetation, generally less abundant in this lake than in Robinson Lake, occurred in lesser amounts in the food of these specimens than in those from Robinson. Again the sole possible significance of the food relations to game fishes appears to be in competition for food.

Miscellaneous lakes.—The food data for Blanding's turtle from lake habitats in general is based on thirty-two specimens taken during summer months from fifteen additional lakes widely distributed over the Lower Peninsula. The average length of twenty-eight of these specimens measured is 199 mm. (7.8 inches), ranging from 110 to 229 mm. The information from the food contained in specimens in this sizeable series substantiates that of smaller series for Robinson Lake and for East Twin Lake. The data for the two individual lakes is very similar to those of this larger series; this may be taken to indicate an adequacy of the samples. As previously indicated, this turtle is apparently of greater significance to game fishes as a competitor for food than as a predator. In the stomachs crayfishes compose 69.9 per cent of the food and in the intestines, 68.1 per cent. Insects comprise 10.6 per cent of the stomach contents and 20.8 per cent of those in intestines. Some carrion (7.2%) was found in the stomachs.

Non-trout streams.—Although Blanding's turtle is very common in the quiet, marshy areas of several non-trout streams such as the Kalamazoo and Huron Rivers, only four specimens were obtained for study from these habitats. Three contained food solely in their stomachs, and one contained 0.1 cc. of vegetable debris in the colon only. Remains (61.1% by volume) of an unidentifiable bird encountered in one turtle apparently were carrion when taken. There is a duck pen near the place where this specimen was collected and it is probable that the remains represent a bird recently killed by some predator.

Crayfishes (13.5%) and forage fishes (mostly minnows; 23.9%) made up most of the remainder of the food in these three stomachs.

In contrast to the food of the three specimens (from non-trout streams) in which no game fishes appeared, one eight-inch specimen from the White River in Newaygo County (a trout stream) was found by J. C. Salyer, II, to contain in its stomach fifteen brown trout averaging three inches in length with a total volume of 57.9 cc. Also present in the stomach were two Johnny darters, two snails, and one crayfish (*Cambarus virilis*). The colon held traces of trout, caddisfly larvae, and snail remains. Although this individual was collected in the natural stream, it is possible that it had recently fed in the raceways of the adjacent trout rearing station. This would explain the number of trout present; brown trout of the size taken were being cultured in the raceways at this time.

Fish hatcheries.—From fish hatcheries, as from non-trout streams, the series of specimens available for food study is too small to be of conclusive significance. The six specimens whose food was analyzed were collected during the months from June through August.

The food in the colon of one specimen, the stomach of which also contained food, was composed of 65 per cent insect remains and 35 per cent vegetable debris.

Although game fishes (87.5%) made up most of the volume of the stomach contents only two of the six specimens contained such fishes, six in the stomach of one individual and one in that of another. These two turtles were from the trout raceways of the White River Rearing Station. The remaining three specimens, from bluegill and forage-fish ponds, had not eaten any of the fishes being propagated. Because of lower concentration, fish were probably somewhat less available (and thereby less vulnerable) in these ponds than in trout raceways. Crayfishes composed 6 per cent of the food of these individuals.

Carl L. Hubbs has demonstrated (unpublished data) the ability of Blanding's turtle to capture and eat several minnows in a short period of time in a forty-gallon aquarium. The conditions of his experiments were very much like the conditions in the narrow confines of raceways. This evidence and that from the food analyses seems to indicate that this turtle should be removed and excluded from fish rearing waters. Means by which this may be accomplished have been described by Lagler (1939).

ANNOTATED LIST OF THE ITEMS IN THE FOOD OF SIXTY-SIX BLANDING'S TURTLES

Game fishes.—Seven eastern brook trout (*Salvelinus f. fontinalis*) had been eaten by one of the turtles from a fish hatchery. Other game fishes eaten included: 2 yellow perch, 2 sunfishes, and 3 centrarchids.

Forage fishes.—Six muddlers (*Cottus bairdii*) had been eaten from non-trout waters. A brook stickleback (*Eucalia inconstans*) was found in a Blanding's turtle from East Twin Lake that had apparently been feeding in or near the trout stream tributary to this lake.

Fish eggs.—Unidentifiable fish eggs numbering 111 were found in the stomach of a specimen from East Twin Lake.

Birds.—Unidentifiable fragmentary remains of two birds were found in one turtle each. It could not be determined whether or not these birds had been killed by the Blanding's turtles but it seemed unlikely that they had been.

Carrion.—Identified as carrion were the remains of a yellow perch and of another fish in one turtle each.

Leeches.—Hirudinea were represented by two individuals.

Crustaceans.—Twenty scuds (*Gammarus*) were found. Crayfishes (*Cambarus*) numbered 147; some were referable to *C. virilis* (36) and to *C. propinquus* (67).

Insects.—Insects, in addition to unidentifiable and fragmentary remains, were represented by a large variety of kinds and in considerable numbers as follows: *Hexagenia* nymph, 1; *Anax junius* nymphs, 27; *Aeschna* nymphs, 20; *Epicordulia princeps* nymphs, 4; *Libellula* nymphs, 176; *Sympetrum* nymphs, 4; *Leucorrhinia* nymphs, 11; *Celithemis elisa* nymphs, 2; *Celithemis* sp. nymphs, 80; unidentifiable dragonfly nymphs, 183; *Enallagma* nymph, 1; damselfly nymph, 1; adults of *Belostoma*, 5; adults of *Belostomatidae*, 9; *Lethocerus americanus*, 2; adults of *Pelocoris*, 2; *Haliplus* adult, 1; *Dytiscus* adult, 1; *Acilius* adult, 1; other dysticid larvae and adults, 14; hydrophilids, 3; chrysomelids, 1; other beetle, 1; *Neuronia postica* larvae, 2; *Neuronia* sp. larvae, 2; larvae of *Leptocerinae*, 2; leptocerid larvae, few; limnephilid larvae, 2; caddisfly larvae, several; pyralid larva, 1; lepidopteran larva, 1; larvae of *Stratiomyidae*, 6; other dipteran, 1.

Snails and clams.—Mollusks were represented by one or a few of each of the following: *Lymnaea palustris*, *Helisoma trivolvis*, *Helisoma antrosom*, *Gyraulus parvus*, *Physa sayii*, *Valvata tricarinata*, *Amnicola*, *Anodonta*, *Sphaerium*, *Pisidium*, and several unidentifiable fragments.

Plants.—Lower plants present were filamentous algae, *Chara*, *Nitella*, and a little moss. Flowering plants identified were *Typha*, *Potamogeton*, *Najas*, *Spirodela polyrrhiza*, *Lemna minor*, *Ceratophyllum demersum*, *Ranunculus*, *Myriophyllum*, *Cornus Amomum* seeds, and *Bidens* seeds.

Vegetable debris.—Fragmentary plant remains not referable to any taxonomic groups were often found.

SUMMARY AND CONCLUSIONS

A summary of the food contained in fifty-one stomachs and forty-one colons of sixty-six Blanding's turtles collected from wild (natural) waters is given in Table 5 and in Fig. 8. The food habits data for the six individuals from fish hatcheries are of course not included. Because of the possibility that the specimen taken from the White River had recently fed at the rearing station, it also is omitted here.

TABLE 5.—The Food of Blanding's Turtle in Natural Waters in Michigan.

Based on fifty-one stomachs containing 195.8 cc. of food, and forty-one colons containing 140.7 cc. of food, from 66 turtles, collected on seventeen lakes and two non-trout streams. One specimen from a trout stream and six from fish hatcheries not included.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Game fishes	1.6	5.9	TRACES	7.3
Forage fishes	2.7	5.9
Fish remains	0.7	7.8	TRACES	7.3
Bird remains	5.6	2.0	1.8	2.4
Carrion	4.7	5.9
Leeches	0.1	3.9
Crustaceans	56.6	74.5	60.1	85.4
Insects	21.4	54.9	30.3	68.3
Molluscs	2.6	17.6	0.5	12.2
Cryptogams	1.2	21.6	TRACES	36.6
Phanerogams	0.5	31.4	0.3	29.3
Vegetable debris	2.2	39.2	7.0	51.2

Crustaceans, almost entirely crayfishes, make up about one-half of the food of Blanding's turtles in Michigan. More than one-fourth of the food appears to be insects. Miscellaneous invertebrates and vegetable matter compose the remaining fourth of the food. Though it may be concluded that this species is omnivorous as was found also by Cahn (1937) and by Conant (1938), it is interesting to note how restriction to what may be termed an essentially carcinophagous and insectivorous feeding habit involving hard-bodied food organisms causes a close agreement of figures for stomach and colon contents data (Table 5). This is in marked contrast to what has been shown for the somewhat more omnivorous snapping turtle, in which the contents of the stomach and colon are markedly different.

In the annotated list are recorded the details as to the number and kinds of food organisms encountered in lake and stream habitats and at fish cultural stations. The numerical dominance of the food by crayfishes and insects substantiates the findings as seen in Table 5 and reported for Robinson, East Twin, and other lakes. Regarding the food of this turtle, either the volumetric method or the numerical method of food analysis would have given approximately the same picture. By numbers, however, insects are predominant whereas by volume crayfishes come to the front.

As for other aquatic turtles, it would be desirable to have additional information on the relation of this species to nesting game fishes, particularly to centrarchids. This is suggested by the discovery of 111 fish eggs in the stomach of an individual from East Twin Lake.

On the basis of the specimens studied, it seems that on natural waters the principal significance of Blanding's turtles to fish production is reflected in the diet of aquatic invertebrates which this turtle and fishes have in common.

TERRAPENE CAROLINA (Linnaeus)—Box Turtle

Range and Size.—In Michigan the box turtle is known only on the Lower Peninsula in scattered counties to the south and west of an imaginary line drawn from Detroit to Grand Traverse Bay. The average length of the species is less than 152 mm. (6.0 inches).

Habits and Habitat.—The frequent and usual occurrence of the box turtle on land is common knowledge. Only a few of many investigators who have studied this species mention its occurrence in or near streams, swamps, or small, woodland pools.

The specimens which I have collected in Michigan were found on land, near water. On May 2, 1937, I took two individuals in a pasture about fifty feet from a small stream on low, moist ground which was covered with close-cropped grass in St. Joseph County near Three Rivers. The species is particularly common in the lower grounds of the sandy hill-country in Van Buren County near Alma in the vicinity of the Wolf Lake State Fish Hatchery. In this region it shares a habitat in which the hognose snake (*Heterodon contortrix*) and the blue racer (*Coluber constrictor flaviventris*) are also common. Several specimens have been encountered on the sand dykes between ponds at the hatchery.

Food and Feeding Habits.—Holbrook (1842: 25) recorded that the food of the box turtle is composed of insects, crickets and so forth. Allen (1870: 262) found one that had just eaten half the pileus of a very large *Agaricus*. Latham (1916) and Nichols (1917) also report eating of mushrooms. Abbott (1884: 252) reported the species to be omnivorous, including earthworms and strawberries, dewberries, and windfalls from fruit-trees in its diet. Blatchley (1899: 550) twice surprised adults feeding on ripe "papaws." Cahn (1937: 95) writes that vegetable matter predominates in the food of this species and Conant (1938: 139) has observed it to eat earthworms, grubs, crayfish, fish, frogs, salamanders, meat, lettuce, spinach, cabbage, blackberries, blueberries, bananas, tomatoes, several species of fungi, etc., and carrion such as dead birds or amphibians.

Surface (1908: 177) has made the only detailed laboratory study of the food of the box turtle. He analyzed the food for forty individuals and found that in 62 per cent of those containing food vegetable matter was present, in which berries and seeds were conspicuous. Eighty per cent contained animal material. Prominent among the animals identified were snails in fourteen individuals, grasshoppers in seven, moths in nine, and beetles in ten.

SUMMARY AND CONCLUSIONS

It is apparent from accumulated knowledge that this omnivorous and essentially terrestrial turtle can be of no concern in fish management. The idea that it might be a liability in truck or flower gardens, suggested by other workers, is not supported by observation.

GRAPTEMYS GEOGRAPHICA (LeSueur)—Map Turtle

Range and Size.—The map turtle in Michigan is limited in its distribution approximately to the southern half of the Lower Peninsula, although it is unknown from several counties within this area (Fig. 3). The species attains a size as large as 253 mm. (10.0 inches). The average length through the carapace of twenty-one of the specimens studied for food is 157 mm. (6.2 inches), ranging from 91 to 229 mm.

Habitat and Habits.—Many workers have published information on the habitat of the map turtle in various parts of its range such as "lakes" (Conger, 1920; Cahn, 1937; Conant, 1938; Garman, 1892; Gloyd, 1928; Newman, 1906), "rivers" (Thompson, 1915b; Cahn, 1937; Conant, 1938; Garman, 1892; Henshaw, 1904; Morse, 1904), "sloughs" (Cahn, 1937) and "flood-ground pools" (Garman, 1892).

I have seen this preeminently aquatic species basking on logs, two and three deep, with mid-western painted turtles, in sloughs and backwaters of the St. Joseph River near Colon. It is a common species in the quiet waters of the Huron River near Ann Arbor, and it inhabits river-mouth lakes such as White and Muskegon Lakes where I have trapped specimens. The map turtle was found associated with the musk, snapping, Blanding's, mid-western painted, and soft-shelled turtles in many lakes, large and small, in the southern part of the state.

Food and Feeding Habits.—No detailed food studies of the map turtle have been reported; several records, however, exist. Garman (1890: 91) found the food to consist exclusively of mollusks, in young specimens consisting of *Valvata tricarinata* and other thin-shelled species, in adults of larger and thicker shelled forms. Newman (1906: 139-140) reported that *Graptemys* feeds exclusively upon the flesh of a species of viviparous snail. The stomachs of more than twenty specimens contained the bodies and opercula of these mollusks and when the turtles were kept in aquaria the opercula were very numerous in the excreta. Surface (1908) found a specimen to contain only crayfishes. Bishop (1921: 81) confined a specimen in a box and it disgorged several large and many small fragments of the fresh-water clam, *Unio complanatus*. Roddy (1928: 27) wrote that the food of this species is chiefly mollusks and crayfishes but added that water lilies and perhaps other succulent water plants may enter into its diet. Conant (1938: 144) records the following items in the food: crayfish, fish, aquatic insects, carrion, and snails.

Specimens in my laboratory and in the reptile pit at the University Museums in Ann Arbor take chopped beef-heart, fish, and lettuce, as did those reported by Conant (*loc. cit.*). Regarding time of feeding, I have seen specimens feeding during most daylight hours and at night on weedless bottom of sand and marl in Wolf Lake (Van Buren County) and in East Twin Lake (Newaygo County).

My more detailed studies of the map turtle are based on twenty-seven specimens which contained food either in the stomach or colon or in both. These turtles were collected from four inland lakes, two river-mouth lakes,

and two trout and two non-trout streams during the months of May through August (Fig. 3). Six additional specimens were from unknown dates and localities in Michigan. Owing to the fact that the series is so small, no ecological grouping of the material has been made. A summary of food analyses of all the specimens is given in Table 6 and details of numbers and kinds of items eaten in the annotated list.

ANNOTATED LIST OF ITEMS IN THE FOOD OF TWENTY-SEVEN MAP TURTLES

Game fishes.—Identified were one small yellow perch and centrarchids.

Forage fishes.—Three specimens of the northern blacknose shiner were found.

Carrion.—Identified as carrion were the remains of three trout.

Crayfishes.—Of the crushed remains of 13 crayfishes (*Cambarus*), 7 were *C. immunis*.

Water mites.—Three Hydracarina were present.

Insects.—Insects eaten by map turtles were often in immature stages: *Stenonema* nymphs, 2; nymphs of Ephemeridae, 2; nymphs of Zygoptera, 8; hydrophilid larva, 1; elmids, 274; scarabiids, 278; unidentified beetles, 7; lepto-cerid larvae, 68; limnephilid larvae, 58; larvae of *Helicopsyche*, 28; unidentified caddisfly larvae, 70; larval chironomids, 4; larva of *Chironomus*, 1; asilid, 1.

Snails and clams.—Mollusks were well-crushed and often largely decalcified when found. Because of this it was often impossible to obtain counts of the numbers of individuals eaten. In order to give some idea of the numerical relations, the approximate numbers were then estimated when possible as "few" (less than 5), "several" (5-12), "many" (12-100), or "very many" (more than 100). Identified were: *Lymnaea catascopium*, 24; *Lymnaea palustris*, 5; *Helisoma trivolvis*, 8; *Helisoma antrosum*, many; *Helisoma campanulatum*, 3; *Gyraulus parvus*, many; *Gyraulus* sp., several; *Planorbula armigera*, 2; *Physa gyrina*, 4; *Physa sayii*, many; *Valvata tricarinata*, 4; *Valvata bicarinata perdepessa*, 2; *Valvata* sp., many; *Amnicola integra*, 5; *Amnicola limosa*, many; *Amnicola lustrica*, many; *Amnicola walkeri*, 5; *Amnicola* sp., many; *Bithynia tentaculata*, many; *Campeloma*, several; *Lioplax subcarinata*, 1; *Goniobasis livescens*, few; *Goniobasis* sp., many; *Sphaerium*, 1; *Pisidium abditum*, very many; *Pisidium* sp., several; *Lampsilis siliquoidea*, several; *Strophitus rugosus*, few; *Anodonta grandis*, several.

Plants.—Plant remains were classifiable as filamentous algae, several *Potamogeton* seeds, *Ceratophyllum*, and vegetable debris.

SUMMARY AND CONCLUSIONS

The game fishes found in map turtles were represented only by the head of a small yellow perch in one stomach and traces of the remains of two centrarchids in one colon, and forage fishes by three northern blacknose shiners in one stomach. The fishes in the stomachs were apparently alive when taken.

The data in Table 6 indicate that crayfishes, mollusks, and insects are

principal foods of this turtle. The broad alveolar surfaces of the jaws of these animals are useful in crushing mollusks and other hard-bodied invertebrates. Evidence of this is the crushed condition of the crayfishes, beetles, snails, and clams in the stomachs examined.

It is not evident whether the small amounts of plant tissue in four colons had been taken primarily or secondarily. The occurrence of several seeds of *Potamogeton* in one colon suggests that perhaps hard-coated seeds of this type are definitely taken as food. The coats of these seeds had been broken open by the action of the jaws, by digestion, or by abrasion from accompanying snail shells.

Numerically the food items are dominated by insects and mollusks. The marl beetles (Elmidae), which appeared in greater numbers than any of the other groups of insects, occurred mostly in one colon, which contained 271. These beetles are very small and are thus far from being as volumetrically significant in the food as the numbers would seem to indicate.

Identifications of mollusks eaten were made as specifically as possible in order to establish not only the predator-prey relationship for the several forms, but also to provide a tool for the use of parasitologists in studying important fish parasites or human pests such as swimmer's itch (*schistosoma dermatitis*). It is evident that in destroying many of the molluscan hosts of such parasites, the map turtle may be a distinct economic asset. This may outweigh some of the competition which it obviously offers to fishes for food.

TABLE 6.—The Food of the Map Turtle in Natural Waters in Michigan.

Based on twelve stomachs containing 38.2 cc. of food and twenty-four colons containing 95.6 cc. of food, from twenty-seven turtles, collected on six lakes, four rivers, and some unknown waters.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Game fishes	1.8	8.3	TRACE	4.2
Forage fishes	11.3	8.3
Fish remains	2.4	8.3	0.6	8.3
Carion	5.0	8.3
Crayfishes	52.4	8.3	13.0	25.0
Water mites	TRACES	8.3
Insects	8.6	41.7	12.0	50.0
Snails	17.3	83.3	57.7	79.2
Clams	1.3	8.3	12.5	37.5
Plants	4.2	16.7

CHRYSEMYS PICTA: BELLII (Gray) × MARGINATA (Agassiz)—Intergrades between Bell's Turtle and Mid-western Painted Turtle

Range and Size.—As shown by Hartweg (MS) *Chrysemys picta* is represented in lakes, ponds, and streams on most of the Upper Peninsula in Michigan by intergrades between *bellii* and *marginata*, whereas the mid-western

painted turtle (*Chrysemys picta marginata*) is restricted to the Lower Peninsula. The eight adult intergrades which I studied for food averaged 146.6 mm. (5.7 inches) in length, ranging from 126 to 129 mm.

Food and Feeding Habits.—Four of the eight intergrades were collected for food study from a small pond about nine miles northeast of Engadine, Mackinac County, on July 17, 1937. The other four were taken from Pickerel Lake, near Marquette in Marquette County on July 27-29, 1937. It is unfortunate that so few specimens were obtained, but the conclusions drawn from extensive material of *C. p. marginata* presumably may apply also to the intergrades. The results of the analyses of the food of the small series of intergrades are given in Table 7.

ANNOTATED LIST OF ITEMS IN THE FOOD OF EIGHT INTERGRADES BETWEEN
BELL'S TURTLE AND MID-WESTERN PAINTED TURTLE

Frogs.—Remains of two frogs (*Rana*) were found in one stomach.

Crustaceans.—Crayfishes present were: *Cambarus propinquus*, 1; *C. diogenes*, 1; *Cambarus* sp., 5. Several Cladocera were also found.

Insects.—Insects were an ephemerid nymph; *Anax junius* nymphs, 2; *Libellula* adult and nymph, 2; *Sympetrum* nymph, 1; unidentifiable dragonfly nymphs, 3; adult of *Lestes*, 1; adult of *Ischnura*, 1; damselfly adult, 1; corixid adults and nymphs, 15; belostomatid adults, 2; *Pelocoris* adult, 1; dytiscid adults and larva, 9; hydrophilid adults, 2; unidentified adult beetle, 1; lepto-cerid larvae, 12; unidentifiable caddisfly larva, 1; sphingid larva, 1; lepidopterous adults, 2; chironomid larvae, 287.

Snails and clams.—Snails present were one *Helisoma trivolvis*, a few *Amnicola limosa*, and a few other individuals. Clams (*Musculium truncatum*) occurred sparingly.

Cryptogams.—Algae identified were *Scenedesmus quadricauda*, *Mougeotia*, *Spirogyra*, and *Hyalotheca dissiliens*. A little moss was also found.

Phanerogams.—Flowering plants were represented by *Potamogeton*, *Sagittaria*, *Nymphaea odorata*, and some unidentifiable fragments.

SUMMARY AND CONCLUSIONS

Insects and their aquatic larvae, and crustaceans, mollusks, and aquatic plants appear to be the principal foods of these turtles. The high value for frogs in percentage by volume is due to the occurrence of the remains of two specimens in one stomach.

It is interesting to note the large numbers of hard-coated seeds of the white water lily (*Nymphaea odorata*) ingested. These mature seeds, 813 in number, make up most of the volume of the plant materials eaten. They appear no different in the colons than in the stomachs, and probably remain viable in

passing through the turtle. This observation and others suggest that these animals may be of ecological significance in the dispersal of water lilies.

On the basis of this material, it appears that the intergrades (between Bell's turtle and the mid-western painted turtle) have food habits much like those of the mid-western painted turtle (p. 302) and that these turtles compete with fish for food, but do not prey upon them.

TABLE 7.—The Food of Intergrades Between Bell's Turtle and Mid-Western Painted Turtle in Michigan Waters.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Frog	42.7	14.3
Crustaceans	6.0	57.1	6.4	57.1
Insects	15.4	85.7	7.7	57.1
Molluscs	8.5	42.9	0.8	28.6
Cryptogams	TRACE	14.3	3.4	28.6
Phanerogams	24.8	57.1	79.9	85.7
Vegetable debris	2.6	57.1	1.9	57.1

CHRYSEMYIS PICTA MARGINATA (Agassiz)—Mid-western Painted Turtle

Range and Size.—The range of *C. p. marginata* has been stated by Bishop and Schmidt (1931: 137) as extending "... from eastern New York through western New York and western Pennsylvania, Ohio, Indiana, and the lower peninsula of Michigan and southeastern Illinois. . . ." (Fig. 5). Average size of adults is 127 mm. (5.0 inches).

Habitat and Habits.—The mid-western painted turtle is the most common turtle on the Lower Peninsula of Michigan, throughout which it is abundant. Very little has been written regarding its habits, whereas the life history and habits of *Chrysemys p. picta* have been rather thoroughly described by several investigators in the eastern states. That there is a close similarity of food habits of the various subspecies and intergrades may be seen by comparing the data which I present with those of Surface (1908) for *C. p. picta* and with those of Pearse, Lepkovsky, and Hintze (1925) for a series of intergrades between *bellii* and *marginata*.

It seems that what Conant (1938: 148) wrote for the mid-western painted turtle in Ohio also obtains for this turtle in Michigan as well as in other parts of its range as described by other authors: they are to be found in almost any locality in which there is sufficient permanent water to hide them and to supply them with food. In Michigan I have collected the turtle from all environments listed by Conant for Ohio (wet meadows, bogs, marshes, woodland pools, brooks, ditches, ponds, lakes) and in addition from a variety of stream habitats. One of the largest catches of this species which I made in an overnight set of one trap was forty individuals. This set was in a bayou of the Muskegon River about seven miles east of Muskegon. The species is very common in the quieter

most common per unit area where a soft bottom supports a luxuriant, though not over-abundant, aquatic vegetation.

Mid-western painted turtles in Michigan have been collected by me from environments where they are associated with musk, snapping, Blanding's, map, and soft-shelled turtles. In lakes the most common associates of the painted turtles appear to be the snapping and Blanding's turtles, and the musk turtle within the limits of its range. In the larger rivers of the southern part of the Lower Peninsula, its habitat seems to be shared for the most part with the map turtle.

Food and Feeding Habits.—In so far as I have observed, the mid-western painted turtle is entirely aquatic in its feeding activities although several investigators claim that the species exhibits certain terrestrial tendencies. Specimens in the wild are active feeders and during summer months they have been observed foraging on the bottom in shallow water at night and in the early morning and evening hours. At mid-day they were usually basking.

Food studies of this subspecies based on smaller numbers of specimens by Newman (1906), Hankinson (1908), Baker (1916), Conant (1938), and Raney (1942) substantiate the current findings.

My food studies of the mid-western painted turtle are based on the stomach contents of 413 specimens from fifty-five lakes or ponds, seven non-trout and four trout streams, and five fish cultural establishments. Collections were made during the months of May through October, mostly in 1937 and in 1938 from localities well-spread over the Lower Peninsula (Fig. 5). The material is doubtless adequate to indicate the food of this turtle, but information on certain special phases of its relation to game fish populations, such as that of predation of eggs and fry, is however, still lacking. Since the number of specimens collected was so large, only the contents of the stomachs were analyzed.

In the following record and discussion of the food habits, the specimens from Wintergreen and East Twin Lakes are considered separately, to facilitate comparison of the food of this species with that of other turtles collected from the same lakes. Individuals from several lakes and ponds have been combined into two groups: (1) those from miscellaneous lakes and (2) those from river-mouth lakes. Additional groups are those from: (1) non-trout streams, (2) trout streams, and (3) fish cultural stations. A summary of the food of this turtle on natural waters is given in Table 8. In the annotated list are presented details of the numbers and kinds of food eaten.

Wintergreen Lake.—A description of this lake has already been given (p. 270). Twenty-one mid-western painted turtles from this lake contained food. Ten measured specimens from this series ranged in carapace length from 94 to 142 mm., averaging 127 mm. (5.0 inches).

Game fishes and forage fishes occurred only once each in this series of specimens. Insects and aquatic vegetation appeared as the principal food. Of the insects, 1387 caddisfly larvae, 919 halipid beetle larvae of the genus *Pelto-*

dytes, and more than 190 mayfly nymphs were the most numerous. Filamentous algae comprised by far the dominant plant material ingested (71.0% of the total volume of food). In three stomachs there were forty-seven wheat grains from food scattered along the shores for waterfowl. Some of the grains were in a very much softened condition in the stomachs, indicating that they were perhaps undergoing digestion.

East Twin Lake.—A brief description of East Twin Lake has already been given (p. 272). The average size for eleven mid-western painted turtles that were measured is 132 mm. (5.2 inches) ranging from 105 to 156 mm. Sixty-two additional individuals trapped in this lake during the summer of 1938 were measured, marked for future recognition, and returned to the water as a part of the population-density and growth-rate investigations being conducted on turtles in this body of water.

A summary of the analyses of the food in the stomachs of the series examined from this lake shows an unusually large percentage composition by volume (16.1%) for game fishes. Since this volume is entirely composed by one young pumpkinseed it is probably not a true index of the food relations. Insects (28.0% of the total volume of food) were almost entirely dragonfly and damselfly and caddisfly larvae. Aquatic vegetation, especially filamentous algae, is the chief component (54.8%) of the food of almost all of the individuals.

River-mouth lakes.—The two river-mouth lakes from which mid-western painted turtles were taken are Muskegon and White Lakes. The general nature of these waters is described on page 273. The thirty-two painted turtles that contained food were collected on the same dates as were the snappers (p. 273); fourteen were obtained from Muskegon Lake and eighteen from White Lake. The average length of these individuals is 124 mm. (4.9 inches) ranging from 32 to 154 mm.

As for the two inland lakes just cited, the food of the mid-western painted turtle in these river-mouth lakes is principally insects and aquatic plants. The insects encountered in greatest volume, numbers, and frequency were larvae of hydropsychid caddisflies and aquatic pyralids. The pyralid larvae averaged forty-three per stomach for each of ten turtles in which they were found. Most of them were in houses made of *Lemna trisulca* which, in itself, is often taken as food by the painted turtle in this and other waters. Filamentous algae and *Anacharis canadensis* made up most of the aquatic vegetation found.

Miscellaneous lakes.—These bodies of water are ecologically diverse, but the 152 turtles studied for food from them have been assembled to demonstrate the average nature of the food consumed by a wide-spread and random sample of the total population in lake habitats in the state.

The average length of 136 specimens in this series is 122 mm. (4.8 inches) ranging from 49 to 185 mm.

A summary of the analyses of the food in the stomachs of 152 individuals shows a predominance of insects (15.1% by volume) and aquatic vegetation

(59.0% by volume), which strikingly resembles that of the specimens from the lakes reported individually. Crustaceans (8.3% by volume), including amphipods, isopods, and crayfishes, and mollusks (11.7% by volume) assume a slightly greater role than heretofore. The total absence of vertebrates in this large series is noteworthy.

Non-trout streams.—The mid-western painted turtles for food study from non-trout streams were mostly obtained from the larger rivers in the southern part of the state. Of the fifty specimens in this series, thirty-three were from Price's Bayou on the Muskegon River about seven miles upstream from Muskegon. Others were from the Kalamazoo, Huron, Clinton, and Shiawassee Rivers. As has been indicated, painted turtles are generally very common in the quiet-water portions of such streams and little difficulty was encountered obtaining the sample for study. The average size of forty-five of the specimens studied is 123 mm. (4.8 inches), ranging from 63 to 159 mm.

A compilation of the food found in this fifty specimens discloses an increase in the amount of crustaceans (11.5% of the total volume of food) over those of the previous lacustrine series. This increase may be due to the greater numbers of these organisms, particularly of crayfishes, that exist per unit area in lotic than in lentic environments. Insects, mostly aquatic nymphs and larvae, retain a position of some importance (9.9% by volume). Both by volume (72.8%) and by frequency of occurrence (in more than half of all the stomachs examined) aquatic vegetation is again exhibited as the chief food.

Trout streams.—Only five mid-western painted turtles were available for food habits study from trout streams. Aquatic insects (particularly caddisflies and blackflies) and their nymphs and larvae are the most important food of the turtle in this type of habitat. Crayfishes and small frogs are also represented.

Fish hatcheries.—Nineteen specimens collected at fish hatcheries contained food. Fifteen measured individuals ranged from 105 to 153 mm., averaging 127 mm. (5.0 inches).

Ten of the turtles in this series were taken from one of the fish rearing ponds at the Sunset Water Gardens (Oakland County) while it was being drained. This pond was being used for the propagation of bait and forage minnows and goldfish. At the time of draining, the turtles were concentrated with very many young fishes near the outlet, in a small pool of water with a surface area less than one-tenth that of the bottom of the pond. The remaining nine specimens were from the bluegill and bass rearing waters at the Wolf Lake Hatchery (Van Buren County), bluegill or forage fish rearing ponds at the Drayton Plains Hatchery (Oakland County), and a trout raceway at the Pentwater Rearing Station (Oceana County). In spite of the fact that all these rearing enclosures are shallow over their entire area and that they contain abnormally high concentrations of small fishes, only a single, small bluntnose minnow represented the propagated species.

Carrian appeared as a food item of some importance by volume but was

entirely composed of the remains of a large bluegill in the stomach of one turtle which was shot while feeding on a dead fish.

Insects taken included some forms, such as mayfly and dragonfly nymphs and caddisfly larvae, which are important as food for the fish being cultured in these waters. To counterbalance this possible liability as a competitor for food, the consumption of predaceous beetles and 1570 mosquito pupae must be recognized as an asset.

ANNOTATED LIST OF ITEMS IN THE FOOD OF 413 MID-WESTERN
PAINTED TURTLES

Game and pan fishes.—Only a very few species of fishes valued for sport were found. They were one of each of the following: yellow perch; largemouth bass; pumpkinseed; black crappie.

Forage fishes.—A bluntnose minnow, an unidentified minnow (Cyprinidae), and remains of four percids, presumably darters, composed the few forage fishes eaten.

Other vertebrates.—Vertebrates other than fishes were represented only by the remains of a frog or toad.

Carrion.—Identified as carrion were fish remains, some identifiable as bluegills.

Miscellaneous invertebrates.—Several different kinds of invertebrates, other than insects, were eaten by painted turtles as follows: earthworms, 9; leeches, 13; scuds (mostly *Hyaella knickerbockeri*), 90; sow bugs (Porcellionidae), 177; crayfishes (*Cambarus*), 37, of which 2 were *C. virilis* and 1 *C. propinquus*; 2 spiders; and 18 water mites including *Koenikea concava*, *Piona pugilis*, and *Piona reighardi*.

Insects.—Insects in considerable numbers and in a large variety of kinds were identified as follows: grasshoppers (Tettigoniidae) numbered 5 and included representatives of the genera *Scudderia*, *Nemobius*, and others; an antlion; mayfly nymphs numbered more than 110 and were principally composed of *Hexagenia*, *Isonychia*, *Ephemerella bicolor*, *Caenis*, and many unidentifiable Baetidae; besides 88 unidentifiable dragonfly nymphs, others (mostly nymphs) were 14 *Gomphus exilis*, 2 *Anax junius*, 5 *Macromia*, 1 *Tetragoneuria*, 2 *Tetragonia*, 1 *Epicordulia princeps*, 14 *Libellula luctuosa*, 1 *Libellula* sp., 5 *Sympetrum rubicundulum*, 8 *Sympetrum* sp., 18 *Leucorrhinia*, 1 *Celithemis elisa*, 61 *Celithemis eponina*; damselfly nymphs and adults were, 45 unidentifiable, 33 *Lestes*, 1 *Enallagma*, 1 *Ischnura verticalis*, 1 *Ischnura* sp., 1 *Argia violacea*, 3 *Argia* sp.; more than 75 adult Hemiptera including 1 *Notonecta undulata*, 3 *Notonecta lunata*, 4 *Plea striola*, 1 *Belostoma*, 12 belostomatids, 1 *Lethocerus*, 24 naucorids, 2 *Pelocoris*, and 24 Gerrids; Homoptera were represented by an aphid; Coleoptera, rather numerous both as adults and larvae of aquatic and terrestrial forms, were 2 adults of *Halipplus*, 1032 larvae of *Peltodytes*, 17 halipid larvae and adults, 18 larvae and adults of the family

Dytiscidae, 1 gyrinid, 1 larva of *Berosus*, 2 hydrophilids, 2 carabids, 1 elaterid, 2 buprestids, 1 elmud larva, 1 lagriid, 1 *Macroductylus*, 2 scarabeids, 3 cerambycids, 2 *Donacia*, 3 chrysomelids, 3 curculionids, and remains of 18 unidentifiable larvae and adults; Trichoptera were present as unidentifiable remains of many larval forms as well as many other larvae classified as follows: 1815 hydroptilids, 24 *Hydropsyche*, 15 *Philoptamus*, 1 *Polycentropid*, 14 *Neuronia*, 2 phryganeids, 17 *Leptocella albida*, 185 Leptocerids, 18 *Stenophylax*, 20 limnephilids, and 1 sericostomatid; miscellaneous lepidopterous larvae and adults numbered 18 but 471 additional ones were pyralids; in addition to a few unrecognizable dipterous larvae, sorted out were 29 *Tipula* larvae and pupae, 25 *Triogma* larvae, 1 tipulid larva, 143 *Chironomus* larvae, 119 other chironomid larvae and pupae, and several ceratopogonid larvae and pupae, 1571 culicid larvae, pupae and adult, 36 *Simulium* larvae and pupae, 3 simuliid larvae, 25 tabanids, 2 *Stratiomyia* larvae, 1 stratiomyid larva, 1 asilid, 1 empidid pupa, 1 anthomyid, 2 calliphorid larvae, and 1 *Sepedon*; of 3 Hymenoptera present, one was referable to the family Tenthredinidae.

Snails and clams.—Except for *Amnicola limosa* of which 107 individuals were found, mollusks were sparingly represented by one or a few of each of the following kinds: *Helisoma trivolvis*, *Helisoma antrosom*, *Physa sayii*, *Valvata tricarinata*, *Bithynia tentaculata*, *Lasmigona compressa*, *Sphaerium sulcatum*, and *Pisidium*. Remains of a few other snails and clams were not referable to any of the above.

Cryptogams.—Lower plants, principally filamentous algae, were represented by quantities of each of the following genera and species: *Volvox*, *Oscillatoria princeps*, *Oscillatoria*, *Lyngbya*, *Ulothrix*, *Cladophora glomerata*, *Cladophora*, *Rhizoclonium hieroglyphicum*, *Pithophora varia*, *Oedogonium*, *Pediastrum boryanum*, *Oocystis*, *Spirogyra* sp., *Spirogyra crassa*, *Nitella*, *Cosmarium granatum*, *Phacus brevicauda*, and *Phacus longicauda*. Also present was a little moss.

Phanerogams.—Flowering plants were mostly the leaves and petioles of aquatic kinds; some, however, occurred only as seeds and are thus indicated: *Potamogeton*, *Najas*, *Sagittaria*, *Anacharis canadensis*, *Vallisneria*, *Zea mays* seeds, *Triticum* seeds, *Peltandra virginica*, *Spirodela polyrhiza*, *Lemna trisulca*, *Lemna minor*, *Polygonum*, *Ceratophyllum demersum*, *Nuphar advena*, *Nymphaea odorata*, *Myriophyllum*, and *Bidens*.

SUMMARY AND CONCLUSIONS

A summary of the food contained in 394 stomachs of mid-western painted turtles from natural waters is given in Table 8 and in Fig. 9. For obvious reasons the material for fish hatcheries is not included here.

These data as well as other observations of earlier investigators, demonstrate conclusively that the mid-western painted turtle species is omnivorous. Insects and other aquatic invertebrates, and aquatic plants, compose the bulk of food of almost all of the individuals studied.

The enumerations and the detailed determinations in the annotated list bring out the ecological inter-relations of predator and prey and facilitate evaluation of the data from an economic point of view. Although the great importance of many kinds of insects in the food is evidenced by the numbers in which they are consumed, the even greater importance of aquatic vegetation is somewhat submerged in this tabulation by the mechanics of presentation. It is interesting to note, for the plant materials, the considerable number of species involved. Additional species have doubtless been overlooked by inability to identify some of the seeds and other plant fragments classified as "vegetable debris."

TABLE 8.—The Food of the Mid-Western Painted Turtle in Natural Waters in Michigan.

Based on 394 stomachs containing 408.5 cc. of food.

Food Item	Composition by Volume (%)	Frequency of Occurrence (%)
Game fishes	1.0	1.0
Forage fishes	0.3	1.5
Fish remains	0.1	0.8
Frog remains	0.4	0.3
Carion	2.5	1.5
Spiders and water mites	TRACES	3.0
Leeches and "earthworms"	0.4	3.4
Crustaceans	5.0	15.5
Insects	19.5	55.1
Molluscs	5.5	15.7
Cryptogams	30.7	58.9
Phanerogams	30.8	48.2
Vegetable debris	3.7	35.5

The number of game and pan fishes consumed by the painted turtles examined by me is insignificant for fish management. Regarding the oft repeated accusation of egg predation by this and other aquatic turtles, this series of specimens offers only negative evidence. Several of the individuals collected near centrarchid nests contained no trace of eggs or fry of these fishes. Members of this species have, however, been seen by Vern Winey of Kalamazoo on bluegill nests, supposedly foraging on the fry in a position which made the turtles appear to be standing on their heads. No specimens were captured to verify these observations but Winey was certain that fry were present in the nests.

On the basis of the data assembled, the mid-western painted turtle appears to have significance as a food competitor of game and other fishes but may hardly be considered a predator of these forms. The conclusions for this species are very much like those for the musk turtle, for Blanding's turtle, and for the intergrades between mid-western painted and Bell's turtles. Without additional quantitative work on kinds and amount of food available and kinds and amounts actually consumed by associated fish species, I cannot estimate the seriousness of the food competition which they offer to fishes.

AMYDA SPINIFERA SPINIFERA (LeSueur)—Soft-shelled Turtle

Range and Size.—In Michigan the soft-shelled turtle is limited to waters in approximately the southern half of the Lower Peninsula (Fig. 3). Large adults may have a carapace length of more than 16 inches but lengths of ten of the specimens studied for food averaged 236 mm. (9.3 inches), ranging from 162 to 407 mm.

Habitats and Habits.—Few authors have published material on the habitat of the soft-shelled turtle, but all agree that the species is most common in slow-flowing rivers, but that it also occurs in lakes and ponds. In Michigan I have collected specimens from a few lakes of diverse types, in company with musk, snapping, Blanding's, painted, and map turtles. Individuals have been seen basking on the sands near the mouth of the St. Joseph River at St. Joseph and the Muskegon River near Muskegon. Specimens have been taken for me from the Grand and Huron Rivers. On the basis of the relative uncommonness of the species in the lakes studied, I am inclined to believe that Conant's (1938: 159) observation for Ohio that the soft-shell is probably more essentially a river turtle than any of the other species in the state may be equally true in Michigan.

Excellent observations and summaries of the natural history of this turtle are those of Newman (1906), Babcock (1919), Evermann and Clark (1920), Cahn (1937), and Conant (1938). These authors mentioned, as I have also observed, that it is characteristic of this turtle to lie partly buried in the loose bottom material in shallow water. It is remarkable for swimming ability and pugnacity, and for its habit of resting or basking at the water's surface, sometimes at considerable distances from shore. True aquatic respiration has been demonstrated for this turtle by Gage and Gage (1886).

Food and Feeding Habits.—Newman (1906: 131-132) reports the species to be voracious and carnivorous, feeding principally on crayfishes and the larvae of large insects. He has watched them, as have I, crawl or swim along the bottom, pushing their snouts under stones and into masses of aquatic vegetation, occasionally snapping up a crayfish or larva that they have succeeded in dislodging. True (1893: 152) reported that soft-shelled turtles include a variety of vegetable matter in their food. Surface (1908) examined two specimens and found both to contain crayfish and one with crushed beetles. Babcock (1919: 424-425) reported fresh-water mollusks (*Anodonta* and *Campeloma*), small fishes, tadpoles, and frogs as the diet of this species.

Food habits in captivity disclose a carnivorous nature as reported by Conant (1938: 160) who observed that captives ate a great variety of food including crayfish, worms, insects, snails, fish, and meat, but none were observed to take vegetable matter. Gloyd (1928) previously had found that captives would take crayfishes and scraps of meat. One young individual of this species which was fed water fleas (*Daphnia*) and canned fish ("Balto") in our laboratory for seven months apparently thrived.

My food studies of the soft-shelled turtle are based on fifteen specimens

which contained food either in the stomach or colon or in both. These turtles were collected from seven lakes and two non-trout rivers in the Lower Peninsula (Fig. 3). Owing to the small number of specimens obtained for study, no separation of the material into ecological units has been attempted. A summary of the analyses of the food contained in the stomachs and colons of these individuals is given in the annotated list and in Table 9.

ANNOTATED LIST OF ITEMS IN THE FOOD OF FIFTEEN SOFT-SHELLED TURTLES

Fish remains.—Fragmentary remains of 1 fish were found.

Crayfishes.—Of 22 crayfishes (*Cambarus*) 2 were *C. virilis*; 2, *C. immunitis*; 9, *C. propinquus*; and 5, *C. robustus*.

Insects.—Excepting adults of two dytiscids and one damselfly, all insects were nymphs as follows: 172 *Hexagenia*, and 41 dragonflies, including 24 of *Gomphus*, 1 of *Anax junius*, and 1 of *Celithemis*.

Snails.—Gastropods were represented by a single unidentified individual.

Cryptogams.—Lower plants were in evidence as small amounts of filamentous algae and a little moss.

SUMMARY AND CONCLUSIONS

The statements of Newman (1906), Surface (1908), and Evermann and Clark (1920) on the importance of crayfishes and insects in the food of the soft-shelled turtle anticipated my findings. The occurrence of algae, moss, and vegetable debris seems to support True's (1893) conclusion that aquatic plants are food for this species. This plant material occurred in such small amounts, however, that I could not be certain that it was taken primarily. That plant matter may at times be an important food for this turtle, however, is evidenced by Surface's (1908) findings of considerable quantities of corn in a specimen which he examined from Ohio.

TABLE 9.—The Food of the Soft-Shelled Turtle in Natural Waters in Michigan.

Based on eleven stomachs containing 45.8 cc. of food and six colons containing 35.3 cc. of food.

Food Item	Stomachs		Colons	
	Composition by Volume (%)	Frequency of Occurrence (%)	Composition by Volume (%)	Frequency of Occurrence (%)
Fish remains	TRACE	1.9
Crayfishes	47.4	45.5	46.7	66.7
Insects	52.4	90.9	53.3	83.3
Snails	0.2	9.1
Cryptogams	TRACE	9.1	TRACE	33.3
Vegetable debris	0.2	27.3	TRACE	33.3

Burrowing mayfly nymphs of the genus *Hexagenia* are the most important insect food of my series of specimens. Dragonfly larvae are next most significant. The remains of the fish found in one stomach may or may not reflect the scavenging habit recognized for this species by Cahn (1937) and others.

The material above reported yields no positive information on the relations of this turtle to fish populations. Cahn's (1937) information on the food of the soft-shell is a mere species list and does not bring out the frequency, volumetric, or numerical relations involved. His list of the fishes eaten, the turtle's known skill in capturing food organisms, and its remarkable natatorial ability as described by Newman (1906), suggest a possible economic significance that has not been evident in the present series. Surface's (1908: 123) assertion that "In devouring Crayfish . . . any creature is objectionable from the fact that it is one of the most important foods of the carnivorous fishes" is perhaps an overstatement. The soft-shelled turtle does very obviously compete, to some extent, with game fishes for food. The data available yield no information on how serious this competition may be.

Economic Relations of Michigan Turtles with Special Reference to Fish Management

Because they are not abundant and because they seldom inhabit game-fish waters and do not customarily feed on fish, the spotted, the wood, and the box turtles can be of no concern in fish management.

The musk turtle, Blanding's turtle, map turtle, painted turtles, and soft-shelled turtle appear to be of far greater significance as competitors with fishes for food than as predator on fishes. That these species may feed upon the eggs and fry of fishes, particularly those of centrarchids, is suggested by the present data, but the extent and effects of such feeding have not been determined.

The snapping turtle preys on game and pan fishes for about one-third of its food but most of the individuals eaten are of a size less than one-half the legal length, and the number taken is probably less than one per feeding. Therefore this turtle appears to be a less important fish predator than heretofore commonly supposed.

By eating large amounts of aquatic vegetation, the snapping and painted turtles are shown to exert some pressure in the cropping of such plants. Where the fish population is limited by a deficient growth of plants, this habit may have a deleterious effect. However, this possible harm to plant beds may be largely offset through the dispersal of higher aquatics accomplished by the passage of apparently undigested seeds through the alimentary canal of turtles.

The aquatic turtles studied are omnivores since they feed on both plants and animals.

The malacophagous habits of the aquatic species, especially the musk turtle and map turtle, may be of significance in reducing the incidence of those parasite-pests of higher animals which inhabit mollusks during stages of their life-cycles.

The food of turtles indicates a possible role in the control of insect pests with an aquatic phase in their life histories. More than one thousand mosquito larvae were found in one mid-western painted turtle.

Snapping and soft-shelled turtles have considerable significance as human food and all other species in the state are edible excepting possibly the musk turtle. It seems justifiable to recommend the conservation of the marketable species by limiting the sizes which may be taken to six inches or more, lengthwise through the carapace, and by setting the mesh of traps at three inches square. The potential food value of all other species and the finding that they are not fish predators suggests that legislation be enacted to prevent the wanton destruction that is often their fate.

The removal and exclusion of turtles from fish rearing waters seems to be called for because of the damage which they may inflict on unusually high concentrations of fish.

Snappers were not found to be serious predators of young waterfowl even in a sanctuary lake and the assertion of many previous workers in regard to waterfowl-snapping turtle relations are regarded as overstatements.

The need for investigation on several additional problems dealing with the economic relations of turtles is apparent. A knowledge of frequency of feeding and rate of digestion would greatly enhance the value of the data already in hand. Detailed study of the extent and effects of predation on eggs and fry of fishes would doubtless be a profitable venture. And there exist numerous other subsidiary problems which have been suggested in the body of the text.

Summary

(Figs. 6-9)

For several reasons it is important in food studies to record for each organism eaten the kind (identified as specifically as possible), the numbers of individuals (determined by actual count whenever practicable), as well as the frequency of occurrence and volumetric relations.

A close similarity (approaching identity) of the data for separate, small series of specimens from ecologically similar habitats provides a criterion for judging the adequacy of the material for any one turtle species.

For each species are given: (1) general range and distribution in Michigan; (2) a summary of the published information on habits and habitat augmented by original observations in Michigan; and (3) detailed analyses of the food and feeding habits. Original data on food and feeding habits and cognate ecological observations are presented for the musk, snapping, Blanding's and mid-western painted turtles. For each of these species, as well as for the wood turtle, intergrades between Bell's and mid-western painted turtles, map turtle, and soft-shelled turtles detailed lists of specifically identified food items demonstrate some of the ecological relations involved.

In the food of the musk turtle fish carrion and aquatic insects, mollusks, and plants are predominant.

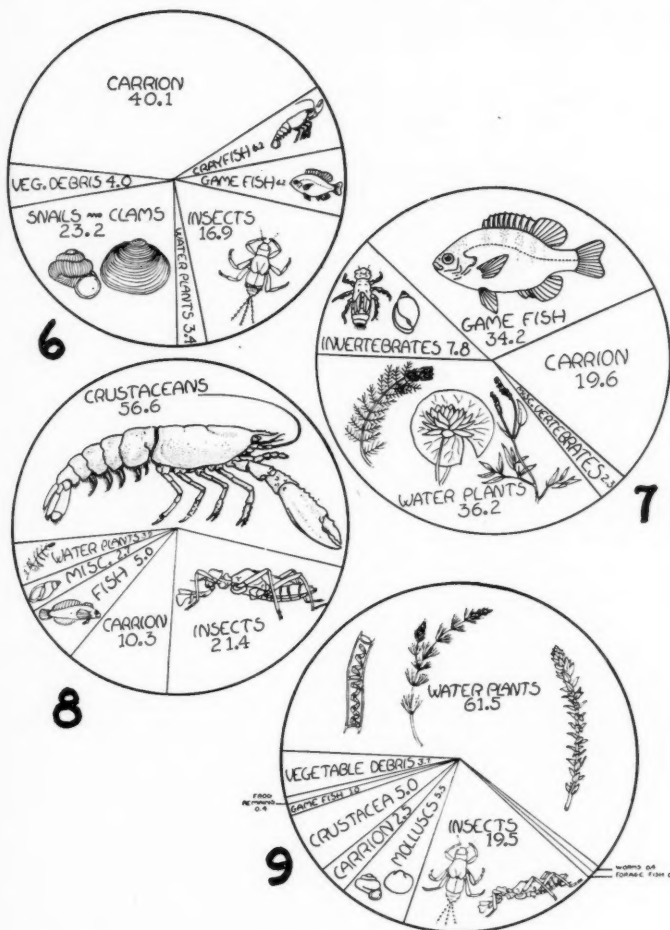


Fig. 9. Percentage composition by volume of the food in the stomachs of 394 mid-western painted turtles.

In contrast to the findings of most previous workers, great significance of aquatic plants in the food of the snapping turtle is established.

The most important food materials found in the stomachs of snapping turtles were water plants, fish, carrion, crayfish, mollusks, and aquatic insects. Invertebrates, principally crayfishes, and aquatic plants dominated the colon contents.

The spotted turtle feeds principally on crustaceans and aquatic insects and their nymphs and larvae.

Wood turtles collected in or near water contained aquatic insect larvae and remains of terrestrial plants.

Crustaceans, mostly crayfishes, and aquatic insect larvae are the outstanding foods of Blanding's turtle.

The box turtle is indicated to feed principally upon succulent land plants and soft-bodied, terrestrial invertebrates.

Crayfishes, mollusks, and aquatic insects are the leading foods of the map turtle.

The mid-western painted turtle feeds mostly upon plants and insects which are to be found in the water. Intergrades between Bell's turtle and the mid-western painted turtle apparently are identical in their food habits with the mid-western painted turtle.

Soft-shelled turtles apparently eat by far more crayfishes and aquatic insect larvae than all other foods together.

It is indicated that, with the possible exception of the snapping turtle, the aquatic turtles of Michigan are probably of greater significance as competitors with fish for food than as predators upon fish. Pending further investigation and with the knowledge that aquatic turtles are beneficial to man because of their scavenger-habits, their suggested role in the control of insect- and parasite-pests, and their potential food value to humans (probably excepting the musk turtle) the conservation of these species is recommended and means for accomplishing this are given. The conservation of the wood and box turtles as currently practiced in New York and New Jersey is also recommended.

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Studies on North American Water Snakes—I *Natrix kirtlandii* (Kennicott)

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Natrix kirtlandii, described by Kennicott in 1856, was rare in collections until a comparatively few years ago. At the time that Hay (1892, 506) stated it was common about Indianapolis, scarcely more than a score of specimens had found their way into museums, and it was nearly thirty years later before the number had passed the hundred mark. Recently, however, this snake has proved to be far from rare in several localities. One such locality, and a particularly favored one, consisted of a few dozen acres of meadowland directly adjacent to the Toledo (Ohio) Zoological Park, with which institution I was associated for a number of years. There, in 1929, I first became interested in this snake and began the studies upon it which I have continued intermittently ever since. In the course of my investigations I have seen in excess of 350 specimens, nearly 200 of them alive, and have made detailed studies upon 267 preserved ones. The results of my studies I set down herewith in the hope that they may shed some light upon a poorly known North American serpent.

History

The literary history of *Natrix kirtlandii* has followed a pattern that is roughly typical of many of the smaller and rarer species of North American snakes. First came formal description, then fragmentary items on habits and habitats, and brief summaries of field notes. There also has been the inevitable inclusion in state and museum lists, and the numerous check lists which have been published in the past eighty-seven years. In the majority of cases in which this snake has been mentioned in print, however, it has scarcely been more than listed or, at best, described in brief, and its habits have been summarized in a few sentences or paragraphs. The paucity of information on *kirtlandii* is attested by the frequency with which authors have quoted their predecessors, meanwhile adding little or no information of their own.

Blatchley (1891), H. Garman (1892), Hay (1892 and 1893), Atkinson (1901), Morse (1904), Ditmars (1907), Ruthven, Thompson, and Thompson (1912), and Conant (1938a) have been the chief contributors to our knowledge of this snake. No detailed summary on *kirtlandii* has been published heretofore.

Taxonomy

Kennicott assigned *kirtlandii* to the genus *Regina*, the specimen on which he based his description agreeing, in all details of scutellation, with Baird and Girard's diagnosis of the genus (1853, 45). He called attention to the marked differences in pattern, however, stressing the fact that *kirtlandii* is a spotted

snake; *Regina*, as constituted by Baird and Girard, contained striped snakes only, namely *leberis* (*septemvittata*), *rigida*, *grahamii*, and *clarkii*, the four striped water snakes indigenous to North America.

Cope, the first subsequent authority to recognize *kirtlandii* in print, placed it, together with Hallowell's *lineatus*, in a new genus *Tropidoclonion* (1860, 340). Later he called attention to the differences in the anal plates of the two species and erected the monotypic genus *Clonophis* for *kirtlandii* (1888, 391).

Jan placed *kirtlandii* in *Storeria* in 1863 (p. 74), and created for it the subgeneric term *Cora*, but finding this preoccupied for a bird genus by Bonaparte, and considering *Ischnognathus* as having priority over *Storeria* (both being proposed in 1853), he adopted the former generic name (1865, 238), a procedure in which he was followed by Boulenger (1893, 286). S. Garman included *kirtlandii* in *Tropidonotus* (1883, 143), while Hay (1892, 505) was the first to assign it to *Natrix*, the large cosmopolitan genus to which it since has been referred by almost all other authors.

Synonymy

1856. *Regina kirtlandii* KENNICOTT, Proc. Acad. Nat. Sci. Philadelphia, vol. VIII, pp. 95-6. (Type locality West Northfield, Illinois. Type specimen USNM 1514).—SMITH, Rep. Geol. Surv. Ohio, vol. IV, 1882, pp. 681-2.—HIGLEY, Trans. Wisconsin Acad. Sci. Arts & Lett., vol. VII, 1889, pp. 165, 174.
1860. *Tropidoclonion kirtlandii* COPE, Proc. Acad. Nat. Sci. Philadelphia, vol. XII, p. 340.—ABBOTT, Cook's Geol. New Jersey, 1868, p. 801.
1863. *Storeria Kirtlandi* JAN, Elenco Sist. Ofid., p. 74.
1865. *Ischnognathus Kirtlandi* JAN, Archiv. Zool. L'Anat. Fis., vol. III, p. 238.
1875. *Tropidoclonium kirtlandii* COPE, Bull. U. S. Nat. Mus., no. 1, p. 42.
1876. *Tropidoclonium kirtlandii* JORDAN, Man. Vert. U. S., p. 176.—YARROW, Bull. U. S. Nat. Mus., no. 24, 1882, p. 131.—DAVIS and RICE, Bull. Chicago Acad. Sci., vol. I, 1883, p. 30.—DAVIS and RICE, Bull. Illinois State Lab. Nat. Hist., vol. I, 1883, p. 41.—BUTLER, Journ. Cincinnati Soc. Nat. Hist., vol. IX, 1887, p. 264.—HAY, Journ. Cincinnati Soc. Nat. Hist., vol. X, 1887, p. 66.—NELSON, Geol. Surv. New Jersey, vol. II, 1890, p. 644.—BLATCHLEY, Journ. Cincinnati Soc. Nat. Hist., vol. XIV, 1891, p. 29.
1879. *Regina Kirtlandii* SMITH, Suppl. Sci. News, I, p. VI.
1883. *Tropidonotus kirtlandii* GARMAN, Mem. Mus. Comp. Zool., vol. VIII, pp. 28, 143, pl. I, fig. 3.
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1888. *Clonophis kirtlandii* COPE, Proc. U. S. Nat. Mus., vol. XI, p. 391.—BROWN, Proc. Acad. Nat. Sci. Philadelphia, vol. LIII, 1901, p. 42.—FOWLER, Rep. New Jersey State Mus., 1906, p. 159, pl. 37.—RUTHVEN, THOMPSON, AND THOMPSON, Michigan Geol. Biol. Surv., 1912, p. 100.
1884. *Regina kirtlandi* GARMAN, Bull. Essex Inst., vol. XVI, p. 24.—GARMAN (H.), Bull. Illinois Lab. Nat. Hist., vol. III, 1892, pp. 273, 275.
1892. *Natrix kirtlandi* HAY, 17th Ann. Rep. Dept. Geol. Nat. Res. Indiana, pp. 504-5.—MCATEE, Proc. Biol. Soc. Washington, vol. XX, 1907, p. 10.—PRATT, Man. Vert., ed. I, 1923, pp. 224-5.—JORDAN, Man. Vert. U. S., 13th ed., 1929, p. 240.—DURY, Zool. Soc. Cincinnati, Quart., vol. I, 1934, p. 10.—SWANSON, Pennsylvania Angler, vol. 4, no. 6, 1935, p. 5, 1 fig.
1893. *Tropidonotus kirtlandi* HAY, Proc. U. S. Nat. Mus., vol. XV, p. 391.
1893. *Ischnognathus kirtlandii* BOULENGER, Cat. Snakes British Mus., vol. I, p. 286.
1895. *Natrix kirtlandii* COPE, Trans. Amer. Philos. Soc., vol. XVIII, p. 215, pl. XXII, fig. 5.—COPE, Rep. U. S. Nat. Mus., 1900, p. 995, fig. 266, pl. 20, fig. 5.—

- MORSE, Ohio Nat., vol. 1, 1901, p. 127.—ATKINSON, Ann. Carnegie Mus., vol. 1, 1901, p. 150.—ECKEL and PAULMIER, New York State Mus., Bull. 51, 1902, p. 379.—MORSE, Proc. Ohio State Acad. Sci., vol. IV, 1904, pp. 104, 132.—NOTESTEIN, 7th Ann. Rep. Michigan Acad. Sci., 1905, p. 116.—STEJNEGER and BARBOUR, Check List N. Amer. Amph. & Rept., ed. 1, 1917, p. 95.—Id., ed. 2, 1923, p. 107.—BLANCHARD, Pap. Michigan Acad. Sci. Arts & Lett., vol. IV, 1925, p. 12.—MYERS, Proc. Indiana Acad. Sci., vol. 34, 1926, p. 288.—NOBLE, Amer. Mus. Guide Leaflet 69, 1927, p. 6.—RUTHVEN, THOMPSON, and GAIGE, Michigan Handbook Series 3, 1928, pp. 72, 101, fig. 32, map.—POPE and DICKINSON, Bull. Publ. Mus. Milwaukee, vol. 8, 1928, pp. 59-60, pl. 15, fig. 3.—WALKER, Copeia, 1931, no. 1, p. 10.—BLANCHARD, Bull. Antivenin Inst. Amer., vol. IV, 1931, p. 96.—HALTOM, Alabama Mus. Nat. Hist., Mus. Pap. no. 11, 1931, p. 63, fig. 25.—PIATT, Proc. Indiana Acad. Sci., vol. 40, 1931, p. 366.—STEJNEGER and BARBOUR, Check List N. Amer. Amph. & Rept., ed. 3, 1933, p. 115.—CONANT, Ohio Journ. Sci., vol. XXXIV, 1934, p. 21.—NETTING, Nawakwa Fireside, nos. 3 & 4, 1935, p. 47.—PRATT, Man. Vert., ed. 2, 1935, pp. 214-5.—SCHMIDT and NECKER, Bull. Chicago Acad. Sci., vol. 5, 1935, p. 70.—ANONYMOUS, Progr. Activ. Chicago Acad. Sci., vol. 7, 1936, p. 1.—NETTING, Proc. Pennsylvania Acad. Sci., vol. X, 1936, p. 28.—DITMARS, Rept. North Amer., 1936, pp. 158, 172, pl. 51.—NETTING, Herp. Leaflet Carnegie Mus., no. 1, 1936, p. 4.—TRAPIDO, Snakes New Jersey, 1937, pp. 7, 36.—POPE, Snakes Alive, 1937, p. 202.—CURRAN and KAUFFELD, Snakes and Their Ways, 1937, p. 262.—SCHMIDT, Ecology, vol. 19, pp. 399, 402, map.—CLAY, Copeia, 1938, no. 4, pp. 174, 176.—CONANT, Amer. Midland Nat., vol. 20, 1938, pp. 5, 15, 20, 74, pl. 9, fig. 2, map.—NECKER, Chicago Acad. Sci. Leaflet 1, 1938, p. 2.—CONANT, Herpetologica, vol. 1, 1938, pp. 138, 140, 143.—CONANT and BRIDGES, What Snake Is That? 1939, p. 95, pl. 16, fig. 47.—STEJNEGER and BARBOUR, Check List N. Amer. Amph. & Rept., ed. 4, 1939, p. 127.—NECKER, Chicago Acad. Sci. Leaflet 10, 1939, p. 2.—Id., 11, 1939, p. 4.—DITMARS, Field Book North Amer. Snakes, 1939, pp. 27, 48, pl. 13.—PERKINS, Bull. no. 16, Zool. Soc. San Diego, 1940, p. 41.—TRAPIDO, Amer. Midland Nat., vol. 25, 1941, p. 680.—SCHMIDT and DAVIS, Field Book of Snakes, 1941, p. 209, pl. 22.—DRIVER, Name That Animal, 1942, p. 383.
1900. *Clonophis kirtlandi* BLATCHLEY, 24th Ann. Rep. Dept. Geol. Nat. Res. Indiana, p. 552.—JORDAN, Man. Vert. U. S. 8th ed., 1899, p. 192.—GIBBS, NOTESTEIN, and CLARK, 7th Ann. Rep. Michigan Acad. Sci., 1905, p. 109.—STONE, Amer. Naturalist, vol. XL, 1906, p. 164.—DITMARS, Reptile Book, 1907, p. 261, pl. LXXX.
1906. *Olonophis kirtlandi* (typographical error) SURFACE, Month. Bull. Div. Zool. Pennsylvania State Dept. Agric., vol. IV, p. 140.
1938. *natrix kirtlandii* (typographical error) CONLEY, West Virginia Rev., vol. 16, p. 15.
1939. *Natrix kirklandii* (typographical error) NETTING, Biennial Rep. Pennsylvania Fish Comm., 1936-38, p. 129.

Type and Type Locality

Kennicott named this snake *Regina kirtlandii* in honor of Dr. Jared P. Kirtland, of Ohio. In keeping with the custom of the time, he failed to designate a type specimen or type locality, simply stating (1856, 96) that "this species has only been detected in Northern Illinois." However, three specimens were presented to the United States National Museum by Kennicott, in 1858, from West Northfield, Illinois, a locality which does not appear on modern maps, but which is near Winnetka in the northern part of Cook County. Two of these specimens still are in the National Museum collection and the third almost certainly is in the collection of the University of Michigan Museum of Zoology.

The original catalogue numbers of the three specimens were 1514, 1515, and 1516. Number 1516 was presented to the Trowbridge Collection at the

University of Michigan in 1859 and is now, almost beyond doubt, number 43928 in the Museum of Zoology of that institution. While this snake no longer bears any designation specifically stating that it once was in the Trowbridge Collection, it is a faded and obviously old specimen, and the collecting data are correct in all details.

Some time after the transfer of 1516 to the Trowbridge Collection, Professor Baird (in his own handwriting) added, on the National Museum register, under 1514, the name *Cora kennicotti* (in error for *kirtlandii*) and placed the word *Type* in the remarks column. This was done probably at the same time that the label (still in existence) was attached to the jar containing the specimens. This reads:

Natural History Survey of Illinois. R. Kennedy (probably in error for Kennicott) 1514 *Cora kirtlandii*. West Northfield, Cook Co.

This jar contained three specimens, each bearing a tin tag stamped (until recently) with the number 1514. One of these is a juvenile (171 mm. in length), the source of which is open to question. In reply to my query regarding it, Dr. Leonhard Stejneger wrote to me, under date of March 25, 1941, as follows:

The stamped tin tags were attached to all the specimens in the collection some time during the late 1870's. Apparently all specimens found in the jar were given the same number, and as the outside label only showed the number 1514, three tags were so stamped and tied to the three specimens in the jar. Possibly the very small and dark specimen had been overlooked when the specimens were first entered on the register (in 1858) and as it then contained no note referring to the number 1516 having been given away, the three tags were attached to the remaining three specimens.

There is also the possibility that the small specimen may have been placed in the jar by mistake at some later time. In any event, its point of origin is doubtful. It would appear, therefore, that the three original Kennicott specimens are the two larger ones that were numbered 1514 in the National Museum collection, and number 43928 in the Museum of Zoology of the University of Michigan.

None of these agrees exactly in scale counts and measurements with the original description, but the larger of the two National Museum specimens comes sufficiently close so that there can be almost no doubt that it is the one upon which Kennicott based his species. It differs from the description in only two respects, these being in the number of subcaudals and in the total length. Kennicott gives 59 for the former, while I count 55. Since he included the anal plate as one of the ventrals (abdominals) he likewise may have counted the terminal spine at the end of the tail as a subcaudal, and the inclusion of small scales at the base of the tail may well account for the rest of the discrepancy. In the matter of length, the specimen is now soft and, as commonly happens, it doubtlessly has stretched. Kennicott gives $19\frac{1}{2}$ inches (496 mm.) as his measurement; the specimen is now 20 inches (509 mm.) in length. The length of the tail, which seldom changes appreciably after long preservation, checks exactly.

On the basis of the above, USNM 1514 (the largest specimen which bore this number) may be considered to be the holotype of *Natrix kirtlandii* and the type locality to be West Northfield, Cook County, Illinois.

Complete scale counts and measurements made upon this specimen are as follows: Scale rows, 19-17, the 4th row being dropped; ventrals 132; subcaudals 55; upper labials 6, lower labials 7; 1 preocular, 2 postoculars; temporals 1-2; 57 dark spots per row of dorsal body blotches; total length 509 mm., tail length 114 mm.; tail/total length .224; sex ♀. The specimen contains several embryos.

Recently, new numbers have been assigned to the two other National Museum specimens which also bore the number 1514. The holotype remains number 1514, the topoparatype has been given the number USNM 115115, and the juvenile of doubtful origin is now USNM 115116.

Material

A total of 267 preserved specimens has been studied. The distribution of these by museums is indicated in the accompanying list of locality records. Distribution by geography is as follows:

Illinois—33; Indiana—24; Kentucky—4; Michigan—8; Toledo, Ohio, and immediate vicinity—85; Ohio, exclusive of the Toledo region—91; western Pennsylvania—19; Delaware Valley—2; locality unknown—1.

The Delaware Valley specimens, because of their doubtful origin (see p. 327), are not included in the summaries and discussions which follow. In preparing Figs. 1 and 2, the few Kentucky specimens have been grouped with those from Indiana for the sake of convenience; the Toledo material has been kept separate to show the extent of variation in a fairly large number of individuals all from approximately the same locality.

A great many of the preserved specimens were examined alive. Nearly one hundred young were born in captivity, the largest of these measured 168 mm. in length at the time of birth; all wild-caught specimens under 170 mm. are also classified as newly-born juveniles and are included, therefore, in the summaries concerned with the very young.

Morphology

The body and tail are moderately slender in juveniles and adult males, and moderately stout in adult females. The head is only slightly distinct from the neck, the widest part being in the temporal region. When seen from above the head narrows gradually to the region of the nasal plates; the rostral is broadly rounded. In profile the top of the head is flat, curving downward slightly over the prefrontals and internasals. The lower jaw is only slightly recessed into the upper one. The eyes are neither large nor protuberant; the diameter of the eye is approximately the same as the distance from the orbit to the nostril; the pupil is round.

Dentition

Teeth in *Natrix kirtlandii* are as follows: Maxillary, 19 to 21, slightly

enlarged posteriorly; palatine, 12 to 14, subequal; pterygoid, 16 to 21, decreasing posteriorly in size; mandibular 23 to 26, largest toward the center of the series.

Sex Ratios and Characteristics

Sex has been determined in 264 specimens, including 84 newly-born young. In the young the ratio is 1 to 1, there being exactly 42 of each sex; among the older specimens females predominate to the number of 96 to 84.

Females attain a considerably greater size than males. The longest specimen (TMS 1660 from East Toledo, Ohio) measured 532 mm. in length when freshly killed; the average of the ten longest females is 492.7 mm. The longest male (TMS 1656 from Jerusalem Township, Lucas County, Ohio) measured 449 mm. when freshly killed; the average of the ten longest males is 421.3 mm. There are twenty females longer than the longest male. Females also exceed males in girth and are stouter in appearance and general body proportions.

The tail length in males averages about 25% of the total length; in females it averages about 22%. In the case of males there is no evidence to indicate a change of tail length correlated with age, but in females the tail averages slightly longer in newly-born juveniles than in older specimens. The extreme ranges and averages are: Adult males (73 specimens) 23.4% to 27.4%, average 25.1%; juvenile males (38 specimens) 23.9% to 27.1%, average 25.4%; adult females (75 specimens) 18.9% to 24.1%, average 21.4%; juvenile females (36 specimens) 20.0% to 24.7%, average 22.9%.

Hemipenes

Each hemipenis, when everted, is bilobed at its distal end and furnished with a smooth saccular tip. The sulcus is simple, its distal end being directed toward the right lobe (in both organs) but terminating in the depression between the lobes. Most of the organ is thickly covered with small spinules which diminish in size distally, leaving the tip smooth. There is one enlarged basal spine lateral to the sulcus, which is followed by 6-10 moderately enlarged spines. The more proximal of these are the largest; distally they diminish to the size of the spinules. A similar group of spines occupies a like position on the other side of the sulcus. A smaller group of spines (4-6) lies on approximately the opposite side of the shaft from the sulcus and at about the same level as the other two larger groups of spines. From each of the latter it is separated by a small smooth, or nearly smooth, area.

The hemipenis (spread open *in situ*) has been figured by Cope (1895, pl. xxii, fig. 5 and 1900, pl. 20, fig. 5).

Scutellation

The scales of the body are imbricate, strongly keeled, and slightly notched posteriorly. The keels are most prominent on the middorsal scales and progressively less so toward the sides of the body. Scales of the first row on each

side are only moderately keeled and are somewhat larger in size than the scales of the other rows. Some scales in the anal region of males bear knobbed keels, as has been stated by Blanchard (1931, 96). Apical pits, of which there are two, are very faint. Often they are difficult to distinguish; in some specimens they appear to be entirely lacking or they may be confined to the scales of a few middorsal rows.

The normal scale row formula is 19-17, the reduction taking place through the loss of the 4th row of scales on each side of the body at a point about opposite the 80th ventral (71st to 96th). In 20% of the specimens the number of scale rows is further reduced to 16 by the dropping of the middorsal row a short distance anterior to the anus. Occasionally the number drops to 15, or even to 14 posteriorly, such reduction taking place in a variety of ways, the 3rd, 4th, 5th, and middorsal rows of scales being dropped in various combinations. In a few specimens the number of scale rows immediately behind the head is 21; in a few others it is only 17.

The data on the ventrals may be summarized as follows: Males (123 specimens)—extreme range 121 to 135, interquartile range 125.6 to 129.3, mean 127.49 ± 0.25 , coefficient of variation 2.19 per cent. Females (131 specimens)—extreme range 123 to 136, interquartile range 128.2 to 131.7, mean 129.95 ± 0.23 , coefficient of variation 2.03 per cent. The coefficient of sexual divergence is 1.91 per cent. The anal plate is divided.

The subcaudals vary as follows: Males (115 specimens)—extreme range 57 to 69, interquartile range 60.5 to 63.8, mean 62.13 ± 0.23 , coefficient of variation 3.92 per cent. Females (119 specimens)—extreme range 44 to 61, interquartile range 52.0 to 56.2, mean 54.10 ± 0.28 , coefficient of variation 5.74 per cent. The coefficient of sexual divergence is 13.8 per cent. The terminal scale at the end of the tail is short and spine-like.

The scales of the head may be described as follows: Rostral twice as wide as high; tongue groove not very deep; underside of rostral with a small crescentic groove paralleling the border of the mouth and running at right angles to the tongue groove. Internasals roughly trapezoidal; prefrontals rounded, their outer portions separating the upper part of the postnasal from the upper part of the prefrontal. Frontal bell-shaped, the apex pointing toward the rear. Supraoculars long and narrow and not projecting above the eye. Parietals broadly in contact, narrowing posteriorly, and widest opposite the line of juncture between the lower postocular and the anterior temporal.

Nasals two, the nostril largely in the anterior nasal; loreal subtrapezoidal, as long as high. Normally a single preocular, twice as high as wide; two preoculars on one side of the head in each of four specimens (out of 257). Postoculars most commonly 2, the lower slightly the larger; twenty-three specimens have 3 postoculars on one side of the head, two have 3 on both sides; one has only a single postocular on one side of the head, another has only 1 on each side. Temporals usually 1-2; 2 anterior temporals on both sides of the head in one specimen, 2 on one side in two; 3 posterior temporals on both

sides in one, 3 on one side in two; a single posterior temporal on both sides in twelve specimens and on one side in twenty-three. Postocular and temporal counts were made on 258 specimens.

Upper labials 4 to 6, the distribution in a total count of 506 is 4(1), 5(147), 6(358); 5th usually the largest, the 3rd and 4th entering the eye. Lower labials 6 to 9, the distribution in a total count of 504 is 6(17), 7(430), 8(52), 9(5); 5th or 6th the largest, the first pair usually meeting on the midventral line; first four usually in contact with the anterior chin shields.

Mental small and triangular. Anterior chin shields slightly smaller than the posterior ones; two or three small scales (end to end) between the anterior chin shields and the first ventral; usually three rows of scales between the first ventral and the last lower labial.

Pattern and Coloration

The dorsal pattern consists of four longitudinal rows of small rounded blotches which are black or very dark brown in color. The blotches of each outer row alternate with those of the adjacent inner row, but the blotches of the two inner rows bear no constant relation to each other. Sometimes they alternate with and sometimes they lie opposite the corresponding blotches of the other inner row. The blotches of the outer rows occupy scale rows 1 or 2, to 6 or 7 on the forward part of the body, and rows 3 to 5 posteriorly; longitudinally they are 2 or 3 scales long. The blotches of the inner rows are smaller; they lie on scale rows 6 or 7, to 9 on the forward part of the body and on rows 6 to 8 posteriorly; longitudinally they are about 2 scales long. In some specimens there also are small dark spots on the lower sides of the body, these alternating with the outer blotches. They lie on the first row of scales, and also may involve the lateral tips of the ventrals and the lower portions of scales of the second row.

Posteriorly, the blotches of the two inner rows may become not only smaller, but more obscure and, in many specimens, the two rows are separated by an unpatterned area of ground color, thus imparting the appearance of a middorsal stripe. In some individuals this stripe is inconspicuous, in others it may be very wide and prominent—as much as seven scales wide in a few. In such individuals the blotches of the inner row may disappear completely toward the posterior end of the body. There is considerable variation in this character but there is a tendency for it to occur most commonly in large females.

The dorsal ground color is brown or brownish grey. The ends of the ventrals and the sides of the body below the blotches are grey. Toward the lateral end of each ventral is a large black spot. These, collectively, form two very conspicuous rows. The center of the belly is red, gradually changing to yellowish, anteriorly, as the throat and chin are approached. The latter are uniform yellow or cream. In many specimens the belly is heavily stippled with grey, in others it may be immaculate (Plate 1, Fig. 4). All degrees of variation between these two extremes are exhibited in the series of specimens studied.

Both the dorsal and the ventral pattern and coloration are continued on the tail, the markings becoming less well defined toward the tip.

The top and sides of the head are black or dark brown, plain or inconspicuously mottled or spotted with yellowish or olive brown. The labials are uniform yellow or cream, except for an area of black extending down from the side of the head onto the last upper labial, this partially or completely cutting off an area of yellow on the last labial. The last and the penultimate lower labials may have one or two small black spots on them.

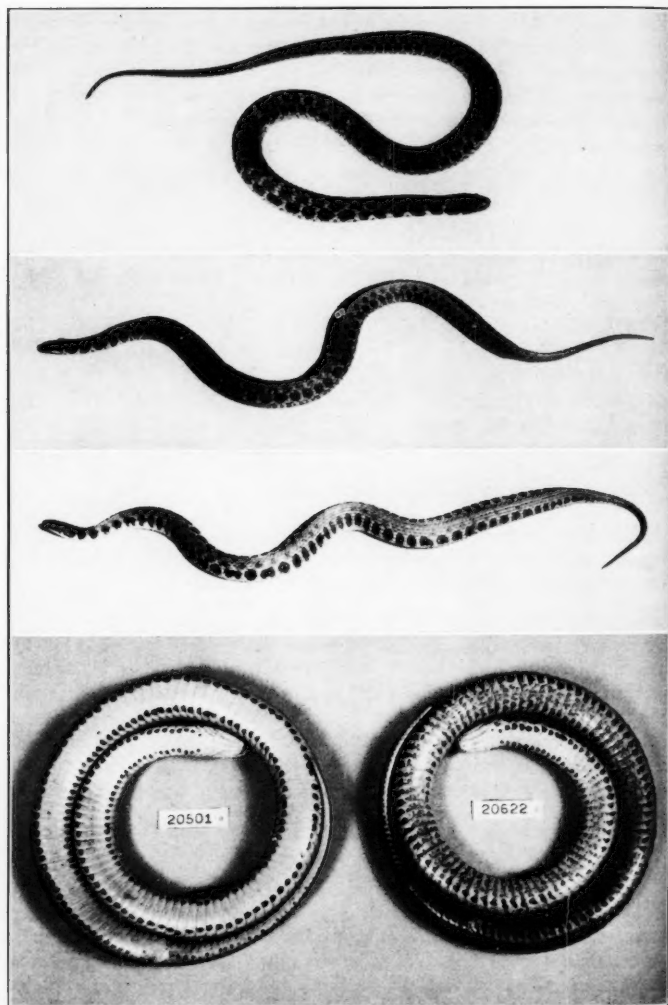
The two large female specimens which are figured (Plate 1, Figs. 2, 3, and 4) were compared with Ridgway's "Color Standards and Nomenclature" (1912) immediately after each had shed its skin. The one from Toledo, Ohio (CM 20622), had the dorsal ground color Russet, anteriorly, and Cinnamon-Brown, posteriorly; flanks of body, Light Neutral Gray; belly, Ocher Red. In the specimen from Wilkinsburg, Pennsylvania (CM 20501), the colors were: dorsum, Chestnut, the dorsal stripe being Auburn; flanks, Mouse Gray; belly, Dragons-blood Red. The dorsal blotches and the large spots on the ventrals were black in each specimen. These two individuals show the approximate extremes of variation in *Natrix kirtlandii* in both coloration and pattern. That such variation is not correlated with geography is indicated by the finding of individuals resembling the Wilkinsburg specimen at Cincinnati, Toledo, and other localities. Normally patterned specimens, in which the middorsal stripe is not particularly conspicuous, are numerous in western Pennsylvania.

Newly born juveniles are very dark and have the dorsum nearly uniform. When the scales are stretched, however, as after the ingestion of bulky food, the pattern usually may be discerned.

The newly born young of the Wilkinsburg specimen (Table 1) show evidences of having uniformly colored dorsal stripes like their parent's. This is abnormal in small *kirtlandii*, but these particular specimens also are abnormal in many other ways. One has a maximum of only 17 rows of scales, several have three rows of subcaudals on at least part of the tail, one has one of its parietals fused with the upper postocular, all have half-scales among the ventrals, and one has twice as many ventrals on one side of the body as on the other side (for a short distance), etc. Three of these snakes were stillborn.

Checks made upon several of the other broods of young born in captivity failed to show any significant differences in scutellation from the general run of adult specimens of *kirtlandii* from the same regions.

The number of dorsal blotches in any one row in *kirtlandii* is approximately the same as the number in either of the other three rows. Counts were made of one row in each specimen (usually the outer row on the left side of the body) counting from immediately behind the head to a point directly above the anus. These may be summarized as follows (170 specimens): Extreme range 43 to 65, interquartile range 50.1 to 55.0, mean 52.52 ± 0.27 , coefficient of variation 6.90 per cent.

PLATE I. Pattern Variation in *Natrix Kirtlandii*

Geographic Variation

There is little geographic variation in *Natrix kirtlandii*, although there is a slight tendency toward reduction in the number of scales toward the eastern part of the range. Thus, the number of ventrals in specimens from Illinois, Indiana, and Kentucky averages higher than in specimens from Ohio and Pennsylvania (Fig. 1). In females the number of subcaudals also averages less in the easternmost specimens, but males do not show this same trend (Fig. 2).

The normal number of upper labials (6) occurs in 95.3% of the cases in Illinois specimens, 69.1% in specimens from Indiana and Kentucky, 73.2% from Toledo, and 53.5% in Ohio, reduction taking place toward the south as well as toward the east. In both Michigan and Pennsylvania the figure is 87%, which probably is not significant owing to the relative scarcity of specimens from those two states. Except in Pennsylvania there is little variation in the number of lower labials and here again it may be the lack of material that causes the discrepancy. The frequencies with which the normal number of lower labials (7) occur are: Illinois 85.4%, Indiana and Kentucky 96.1%, Michigan 87.5%, Toledo 83.3%, Ohio 91%, and Pennsylvania 57.9%.

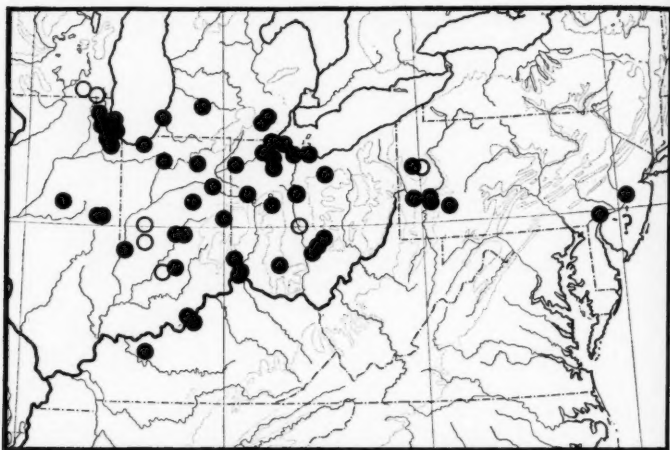
The number of dorsal blotches shows no significant variation which can be correlated either with sex or geography.

The length of the tail in females shows a very slight increase from west to east, the average percentage (tail/total length) being 21.2 in Illinois and 21.8 in Pennsylvania. Populations from the other areas show averages which are progressively greater from west to east. This is in contradiction to what might be expected, inasmuch as the number of subcaudals is slightly less in eastern females. The relative length of the tail in males shows no general trend.

Range

The range of *Natrix kirtlandii* includes extreme southeastern Wisconsin, eastern Illinois, most of Indiana and Ohio, southern Michigan, north central Kentucky, and western Pennsylvania. It also has been recorded from Trenton, New Jersey and Delaware County, Pennsylvania (see map). According to the map "Physical Divisions of the United States," (Fenneman, 1930) this snake occurs in the Central Lowland, Interior Low Plateau, and Appalachian Plateau Provinces and, if the records from the Delaware Valley should prove valid, it also occurs along the eastern edge of the Piedmont Province.

PLATE 1. *Natrix kirtlandii*. Fig. 1 (top). Cornell University Museum No. 3504a, ♂, Toledo, Lucas County, Ohio; total length 355 mm. Photo by A. F. Hallowell. Fig. 2. Carnegie Museum No. 20622, ♀, Toledo, Lucas County, Ohio; total length 452 mm. The rear right portion of the head has been injured. Photo by Mark Mooney, Jr. Fig. 3. Carnegie Museum No. 20501, ♀, Wilkinsburg, Allegheny County, Pa.; total length 469 mm. Photo by Mark Mooney, Jr. Fig. 4. Ventrals of Carnegie Museum Nos. 20501 and 20622. The extremes of variation in pattern in *kirtlandii* (on both the dorsal and ventral surfaces) are shown by these two females. The Wilkinsburg specimen has the mid-dorsal blotches indistinct and has practically no small stipplings on the belly. Such variations, however, apparently are not correlated with geography. Photo by A. F. Hallowell.



Map 1. Distribution of *Natrix kirtlandii*. Solid circles indicate localities from which specimens have been examined; hollow circles indicate additional localities published in the literature. In several instances where a number of localities are very close together (as in the vicinities of Chicago, Cincinnati, and Toledo) not all of them have been plotted. (Recorded on Goode's Base Map 209, Univ. Chic. Press).

According to the "Zone Map of North America," (Merriam, Bailey, Nelson, and Preble, 1910), *kirtlandii* is a member of the Alleghanian and Carolinian Faunas. Specific localities for this species are:

ILLINOIS: (MCZ 13153). * *Champaign Co.*: Champaign (ISNHS 1362); Urbana (ISNHS 1360-1, 1363-4). *Cook Co.*: (FMNH 25293); Chicago (CA 1349, 3862; FMNH 17610; UMMZ 58609.1-10); Chicago Ridge (FMNH 2975, 16127); Grass Pt., Evanston (FMNH 2989, 16126); Northfield (UMMZ 43928); Palos Park (FMNH 23166); River Forest (FMNH 25436-7); West Northfield (USNM 1514, 115115). *DuPage Co.*: Westmont (FMNH 38063). *McLean Co.*: Normal (BMNH 93.1.2.1-2).

INDIANA: (BMNH 93.2.7.3). *Brown Co.*: Washington Twp. (CM 9976). *Floyd Co.*: New Albany (MCZ 5576). *Grant Co.*: Sims (USNM 33845-6). *Kosciusko Co.*: Winona Lake (FMNH 746). *Marion Co.*: (MCZ 14811); Indianapolis (FMNH 21534, 21536; UMMZ 57703, 76826; USNM 31184); Irvington (USNM 17957, 100800-4). *Marshall Co.*: Lake Maxinkuckee (USNM 42591). *Monroe Co.*: (Jordan, 1888). *Montgomery Co.*: Crawfordsville (Hay, 1892). *Porter Co.*: Dune Acres (FMNH 3060). *Putnam Co.*: (Blatchley, 1891). *Randolph Co.*: Winchester (USNM 17953). *Vigo Co.*: Sand Hill (MCZ 14812-3); Terre Haute (Hay, 1892). *Wells Co.*: Vanermon Swamp, Bluffton (UMMZ 53297).

KENTUCKY: *Jefferson Co.*: Louisville (CM 17258; FMNH 25534-5). *Ohio Co.* (CSNH 2427).

MICHIGAN: *Berrien Co.*: Benton Harbor (UMMZ 67264-5). *Kalamazoo Co.*: Kalamazoo (USNM 12627.1-2). *Lenawee Co.*: East of Tecumseh (UMMZ 73216). *Washtenaw Co.*: Freedom Twp. (UMMZ 64390); Pittsfield Twp. (35809-10).

* Abbreviations refer to museums. For full explanations see p. 336.

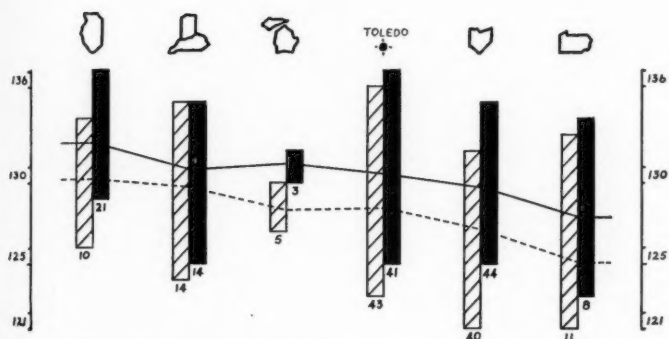


Fig. 1. Geographic variation in the number of ventrals in *Natrix kirtlandii*. The vertical bars indicate the extremes of variation and the cross lines the averages for each area. Data for females are shown by solid bars and solid lines; those for males by cross-hatched bars and dotted lines. The subtended numbers refer to the number of specimens of each sex from each area. The data for Ohio do not include the data for the Toledo region.

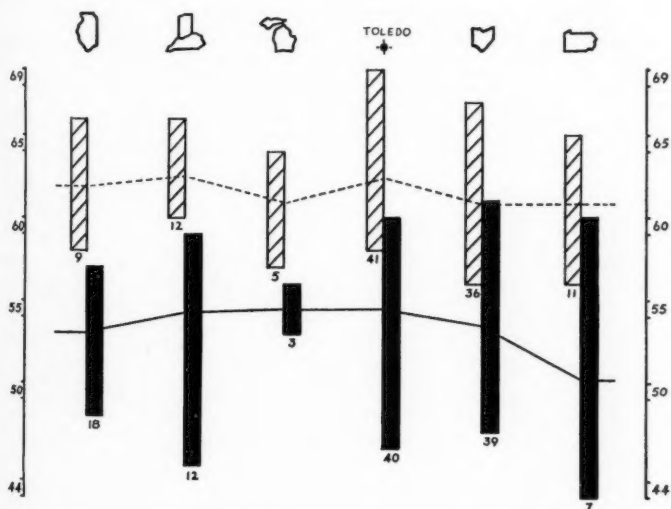


Fig. 2. Geographic variation in the number of subcaudals in *Natrix kirtlandii*. Data, symbols, and general information are the same as for Fig. 1.

NEW JERSEY: Mercer Co.: Near Trenton (ANSP 16802).

OHIO: Auglaize Co.: Lake St. Mary's (OSM 444; TMS 244). Butler Co.: Oxford (MU). Erie Co.: Sandusky (AMNH 3370; MCZ 10011; SHS). Fairfield Co.: Sugar Grove (OSM 40, 94). Franklin Co.: Columbus (Cope, 1860). Hamilton Co.: Cincinnati (CSNH 194, 1453, 1591, 1632, 1664, 1717, 1721, 2032; OSM 458); Avondale, Cincinnati (CSNH 1435A-C, 1461, 1502; OSM 461); Clifton, Cincinnati (CSNH 1632.1-2, 1874A-C, 2017, 2164.1-25, 2346.1-2); Eden Park, Cincinnati (CSNH 852.1-A, 875, 929); Glendale, Cincinnati (CSNH 1651); Mt. Airy, Cincinnati (CM 20630); Westwood, Cincinnati (CM 20603-10). Hancock Co.: Cass Twp. (TMS 600). Highland Co.: Near Hillsboro (TMS 1721); 3 mi. S of Hillsboro (TMS 638-45). Hocking Co.: Salt Creek Twp. (OSM 393.1). Huron Co.: New London (OSM 39). Lucas Co.: East Toledo (OSM 293; TMS 204-6, 1660, 1966); Maumee (TMS 1091); Monclova (BGSU; TMS 2388); Niles Woods, Jerusalem Twp. (TMS 1656); Toledo (ANSP 20601-2; CA 5283; CM 20611-29; CU 3504a-b; TMS 9, 628-35, 1476; UMMZ 68879); Toledo—north end (TMS 2300); West Toledo (TMS 13); Toledo—near Toledo Zoological Park (CM 5278-80, 6677-8, 8088-95; TMS 33-5, 81, 92-7, 379-81, 914, 940, 1092-3, 1196-7, 1222, 1289-1290A, 1647, 1685, 1830, 2382-3, 2419). Logan Co.: West Liberty Twp. (OSM 486). Marion Co.: Marion Twp. (OSM 534). Paulding Co.: Antwerp (TMS 2418). Perry Co.: (OSM 38). Sandusky Co.: 6 mi. NNE of Fremont (TMS 1427). Wood Co.: Bowling Green (BGSU); Maumee River, opposite Waterville (CA 5284-5); Perrysburg (USNM 83449); Tontogany (TMS 396).

PENNSYLVANIA: Allegheny Co.: Coraopolis (CM 1897); Harmarville (CM 4765); Wilkinsburg (CM 20501-10). Butler Co.: Forestville (CM 20598-602); Near Slippery Rock, Wolf Creek (CM 4433); West Sunbury (Surface, 1906). Delaware Co.: (ANSP 5921). Westmoreland Co.: Near Waterford (CM 4885).

WISCONSIN: Kenosha Co.: Fox River, on state border (Hoy, 1883). Walworth Co.: (Higley, 1889).

Natrix kirtlandii also has been recorded from Alabama and West Virginia, both apparently in error. Haltom (1931, 63) included this snake in his "Alabama Reptiles" on the basis of a specimen in the Alabama Museum of Natural History. This specimen no longer can be located and Dr. Henry P. Löding, of Mobile, who originally identified it, recommends that the record be discounted until identification can be verified. I suspect, from Löding's description (in correspondence) that it is not *kirtlandii*.

Conley (1938, 15) records *kirtlandii* from Marshall County, West Virginia, but in response to my inquiry he has stated that the record actually was based on a small *Natrix s. sipedon*.

Schmidt has commented upon the range of *kirtlandii* (1938, 402), characterizing this snake as an endemic of the "steppe" (prairie) peninsula, as outlined by him, Transeau (1935), and others. In the light of further study and more material, I am prepared to support his statement, to give a more critically outlined range and to indicate that *kirtlandii* also exists as a relict in other, adjacent areas.

Throughout the greater part of its range *kirtlandii* is a typical snake of the prairie peninsula, occurring in considerable numbers in many localities and being found associated with such other endemics as *Thamnophis butleri* and *Sistrurus c. catenatus*. Usually it occurs in open, prairie-like habitats. These include wet grasslands, the margins of lakes, streams and swamps, remnants of swamp forest, meadowlands, parks, and other areas from which the original forest long since has disappeared.

In the main part of the range, only a few specimens have been found in woods and many of these have been near small woodland ponds. It is possible,

therefore, that the clearing of the land during the past two centuries has resulted in the creation of numerous habitats suitable for *kirtlandii*, and that this snake is far more abundant now than it was in pre-pioneer days. I already have called attention to the fact that large colonies exist in and near certain urban centers (Conant, 1938a, 77). The sites of these were once largely or entirely forested.

It might be postulated further that *kirtlandii* was common and widespread during the post-glacial period when prairie conditions were at their maximum, and when the hardwood forests of the southeast had not yet invaded the region to the immediate south of the Great Lakes. The coming of the forests probably forced *kirtlandii* to retire, in the main, to the scattered wet prairie areas which continued to exist into modern times. It is also possible that it managed to survive within the forests themselves, in or near woodland ponds or in areas of swamp forest. If this were the case, then *kirtlandii* survived as a relict in those habitats which proved most suitable for it. From many such areas it apparently has spread in recent times.

On the periphery of its present range, especially to the east and south, *kirtlandii* occurs in wooded habitats, but there it is rare and the few colonies which exist may be considered as remnants of a former wider distribution and abundance. Atkinson and Netting (1927, 41) have explained the presence of *Sistrurus* in western Pennsylvania on the basis of the former tongue of prairie which extended eastward from Ohio into that state. Possibly *kirtlandii* arrived in Pennsylvania over the same route. Entrance into that state may be interpreted as a normal expansion in times past, when the pressure of a large and vigorous population may have caused invasion of the territories adjacent to the main range. A similar interpretation may be placed upon the presence of *kirtlandii* in certain hilly, forested areas south of the glacial boundary in Ohio and Kentucky. In all such localities, beyond the prairie peninsula proper, *kirtlandii* appears to be relict and rare. For example, there is the recent discovery of a specimen at Wilkinsburg, Pennsylvania, the first to be found in the Pittsburgh area for thirty-five years.

The two records from the Delaware Valley are difficult to explain. Both are backed by specimens in the Academy of Natural Sciences of Philadelphia and both, presumably, have good collecting data. One, from near Trenton, New Jersey, was caught in 1859 by Dr. C. C. Abbott, and the other, from Delaware County, Pennsylvania, was obtained about 1893 by E. Dutton. It is possible, of course, that both records are in error or that they are based upon escaped terrarium specimens. They both are typical *kirtlandii*, with scale counts and patterns that agree with those of specimens from the main portion of the range.

If it ever occurred there at all, this snake probably is now exterminated in the Delaware Valley. This region has undergone a great degree of settlement and industrialization in the past few decades, and the few habitats suitable for *kirtlandii* may have been destroyed. A reward which I have offered for the capture of a specimen from the general Philadelphia area has gone unclaimed

for over six years. Through the kindness of Dr. Horace Richards and Mr. Thomas MacDowell, a check has been made at the Trenton Museum and the New Jersey State Teachers' College, and apparently there is no evidence to indicate that specimens of *kirtlandii* have been received by these institutions; certainly there are none in their collections now.

If one presumes that the Delaware Valley records are good, then some explanation must be offered on how *kirtlandii* managed to arrive there. One possibility would be that it came through the Mohawk and Hudson Valleys, an avenue of migration which often has been suggested in explanation of the eastward extension of the ranges of many species of animals and plants. The total lack of records from New York and northern New Jersey discount this possibility, unless there has been a southward displacement of the range as a whole, with extinction of the species in the region of the Mohawk Corridor, somewhat as the opposite northward displacement of *Clemmys insculpta* accounts for the absence of this turtle at the southern end of Lake Michigan (Schmidt, 1938, 406).

That climatic conditions may be equally suitable for *kirtlandii*, both in the Midwest and in the Delaware Valley, is suggested by the climate map of North America, based on the Köppen classification (Ackerman, 1941, 107). On this map Dfa climates are shown as occupying a considerable portion of the "prairie and prairie peninsula states," and also a narrow section along the Atlantic seaboard from southeastern New England to north central Virginia. The known range of *Natrix kirtlandii*, including the Delaware Valley records, falls almost entirely within the limits of the Dfa areas as indicated on Ackerman's map.

Habitat

Considerable comment upon the habitat preferences of *Natrix kirtlandii* has been made in the section on range. It should be stressed again, however, that this snake is essentially an inhabitant of open country, a fact that is beclouded in the literature as a result of the frequent repetition, by later writers, of Kennicott's statement that his specimens were taken in woods. *Natrix kirtlandii* does occur in woods, but it is far more abundant in prairie-like situations. Recent collecting bears this out and statements to the same effect have appeared in print. H. Garman (1892, 275), for example, wrote that he had never seen it elsewhere than on the open prairie.

More specimens of *kirtlandii* were taken in a comparatively small area directly adjacent to the Toledo Zoological Park than in any other one locality. This area, a few dozen acres in extent, was practically undisturbed by human beings for many years, since it was somewhat removed from nearby highways, streets, and roads. The terrain was nearly level and was crossed by a railroad along one side. In early spring it was quite wet, water often standing in some places to the depth of a foot or more; during midsummer it usually was quite dry and dusty. Originally it had been partially wooded, but at the time of my residence in Toledo, it was overgrown with weeds and it obviously had been cleared for a considerable number of years; it apparently had been farmed at

one time. The Miami and Erie Canal ran along one side and may have served as the highway over which *kirtlandii* penetrated into the area subsequent to its deforestation. Recently this area has been greatly disturbed by the building of a boulevard where the canal used to be.

Another particularly favorable habitat was in Cincinnati where *kirtlandii* was found in the public parks, in ravines, along the smaller watercourses, and even far up on the hillsides.

No specimens were taken along the beaches of the Great Lakes, a habitat in which *Thamnophis butleri* occurs occasionally. None were found in sandy areas, such as among the fossil dunes which mark the limits of former post-glacial lakes, and none were secured in the "Oak Openings," the extensive sandy area west of Toledo, in which a considerable amount of collecting has been done. Most of the records for *kirtlandii* are in the larger river valleys, although many were found at considerable distances from streams. This snake is most abundant in the portion of its range which has been glaciated; it is much less common in the unglaciated regions.

The altitudes of a majority of the localities in which *kirtlandii* has been taken have been approximated by consulting Gannett (1906). While most of the altitudes given in this volume are those of conspicuous landmarks in the various towns, they at least provide a rough idea of the altitudinal range of *kirtlandii*; much of the territory in which this snake occurs is relatively flat. The lowest elevations are at New Albany, Indiana (367 to 460 ft.), Louisville, Kentucky (394 to 457 ft.), Terre Haute, Indiana (485 ft.), and Cincinnati, Ohio (481 to 552 ft.). The highest elevations are at Waterford, Pennsylvania (1192 ft.), Hillsboro, Ohio (1063 to 1129 ft.), West Liberty, Ohio (1099 ft.), and Winchester, Indiana (985 to 1089 ft.). The two localities in the Delaware Valley are: Trenton, New Jersey (9 to 60 ft.); the Delaware County record is indeterminate as to exact locality, but Chester and Media, the two principal cities, are 22 and 210 ft., respectively, and much of the county has an elevation of about 400 ft.

Habits

Natrix kirtlandii is far less aquatic than the other North American members of its genus. While it swims readily and appears well able to take care of itself in the water, it usually occurs in a wet meadow type of environment rather than in the water itself. Its habits, in general, are much more similar to those of *Thamnophis butleri*, *Thamnophis s. sirtalis*, and *Storeria dekayi* than they are to the many species of *Natrix* with which I am acquainted both in the field and in captivity.

While shunning the larger bodies of water, with their quota of potential enemies, *kirtlandii* apparently must have moist surroundings in order to exist. Thus it frequently is found inhabiting the environs of small ponds, streams, bogs, and woodland pools, many of which, however, are of a temporary or seasonal nature. In the more open types of habitats its presence usually is

associated with the amount of precipitation, its being abundantly in evidence during and after rainy periods and absent during droughts. What becomes of it is not known, although presumably it retreats to less dry surroundings below ground, and even may go into temporary aestivation. As in the case of most small snakes, loss of water from the body tissues is a serious matter, resulting in reduced vitality and even death, if continued too long. Utilization of moist habitats and a marked propensity to remain in hiding, out of the sun and open air, are the best methods of combating desiccation. *Natrix kirtlandii* has both of these traits well developed.

Of the specimens for which adequate habitat data are available, very few were found out of hiding. Almost all were under stones, boards, logs, or other objects which lay sufficiently close to the ground to conserve the moisture beneath them, and which probably also served to provide a safe retreat from large enemies. Most of the few which were discovered in the open were abroad in the spring. Several authors have commented upon the secretiveness of *kirtlandii*, among them being Blatchley (1891, 29) who stated: "It must be nocturnal in its habits, as every one of the half dozen or more specimens which I have seen were found coiled beneath logs or stones, and usually close to small streams." Probably *kirtlandii* does most of its prowling at night when there is less danger of desiccation and when earthworms—its favorite food—are also apt to be in the open.

There is evidence of marked seasonal variation in the apparent abundance of *kirtlandii*, as has been indicated in a previous paper (Conant, 1938b). Specimens are much more apt to be found in the spring than at other seasons, 43% of those from the Toledo area having been caught in April and 18% in May—these being the two most productive months. Collecting dates are lacking for a great number of the museum specimens which have been examined, but a tabulation of those available shows that the optimum time for obtaining this species, as a whole, is in May. A secondary peak in the autumn also has been noted. Probably temperature, precipitation, mating activities, the search for food after the hibernation period, the activities of collectors, and the lack of covering vegetation in the early spring, all are factors contributing to such a marked seasonal variation in the acquisition of specimens. Males were most numerous in spring collections, probably thus reflecting the more active habits of this sex in the early part of the season. Most specimens found in July and August were gestating females.

When conditions are suitable, *kirtlandii* may be encountered at almost any time of the year. Specimens have been collected in every month except December. Apparently, like certain other snakes, they may be roused to activity rather easily and are apt to be found on mild days, even in midwinter. Hay (1892, 506) mentions seeing one on January 25, and specimens have been collected in Ohio in both January and February. This snake probably hibernates underground in the same areas which it frequents during the active season. A number of individuals, found in the early spring, were coated with mud and were still sluggish from the cold. All were taken in open meadowland

where they apparently had spent the winter. Hay (*loc. cit.*) states that "on the 21st of March, one was dug out of the mud on the margin of a pond." Some evidence is at hand to the effect that *kirtlandii* congregates in denning areas during hibernation, just as *Storeria dekayi* is known to do (Noble and Clausen, 1936). Although no actual "dens" have been found, numerous specimens have been taken in certain small restricted areas which seemed particularly favorable to this snake.

Numerous natricine snakes have the ability to flatten their bodies when alarmed, but none appears to have this characteristic developed to such a remarkable degree as *Natrix kirtlandii*. Some specimens can make themselves look almost ribbon-like. The tail is not compressible, or only slightly so, and when the body is flattened it is possible to tell at a glance just where the tail begins. After assuming the flattened position these snakes frequently remain rigidly immobile until touched or otherwise disturbed. Immediately thereupon there is an erratic wriggling which makes them difficult to capture and to hold. When excited they use vigorous undulations in crawling and seem to expend considerable energy for the amount of progress made; in this respect they somewhat resemble *Thamnophis butleri*, which is noted for its peculiar method of locomotion when under stress. Captives remain nervous and alert, often thrashing about in their cages when annoyed and seldom becoming accustomed to handling. Many specimens will strike, but with their mouths closed. They almost never bite, even when handled roughly. On several occasions larger snakes were introduced into cages containing one or more *kirtlandii*. In each case the latter showed evidence of alarm, flattening themselves, hiding their heads under their bodies or objects in the cages, and lashing their tails back and forth. This reaction was produced by introducing specimens of *Natrix s. sipedon*, *Lampropeltis t. triangulum*, and a large *Eumeces laticeps*.

There is very little in the literature on the subject of food other than a few mentions about earthworms and much speculation on what *kirtlandii* "probably" eats. Atkinson (1901, 150) stated that one he had "freely ate slugs in captivity," and Ditmars (1907, 1936, and 1939) made the assertion that *kirtlandii* feeds upon salamanders, small frogs, toads, and fishes. During the past several years I have kept approximately one hundred of these snakes in captivity, and of this number about half refused all food. The others readily ate earthworms, and on the few occasions when small slugs were available, these molluscs also were accepted readily. Two or three snakes ate the chopped fish which was furnished to most of them, but none showed interest in small frogs, toads, or salamanders. On several occasions small amphibians of several species lived for weeks in the same terrariums with specimens of *kirtlandii* without being molested. That the snakes were hungry at the time was attested by the alacrity with which they attacked earthworms, an activity in which they usually were joined by their amphibian cage mates. Three freshly-caught individuals of *kirtlandii* disgorged earthworms and another disgorged a slug. In its liking for this type of food *kirtlandii* also shows a marked resemblance to such other small terrestrial snakes as members of the genera *Storeria*, *Haldea*, etc., which live largely on similar fare. Its disinterest in amphibians and fish

is in marked contrast to the feeding habits of most other North American species of *Natrix*, which exist chiefly on vertebrate prey.

Of the considerable number of specimens of *kirtlandii* which were kept in captivity not a single adult or other wild-caught individual survived over the winter months. Many, collected in the early spring, ate readily all summer and fall and then suffered a loss of appetite during cold weather, despite the fact that they were kept in heated cages. It is suggested that one of two factors, or both, may have contributed to the deaths of these snakes. The first is the interruption of the normal rhythm of the seasons, by the skipping of the period of hibernation. The snakes did not eat during cold weather but remained active, thus using up their reserves. The second factor may have been a dietary deficiency, even in the case of the greediest eaters, since almost all lived exclusively upon earthworms. Some elements of food, perhaps certain vitamins, may be more plentiful in the bodies of slugs, or other items in the diet of *Natrix kirtlandii*, than in earthworms. It was impossible to supply such other food except on rare occasions. Years of experience indicate that many snakes which are given, and which accept, a variety of food, usually live longer than their cage mates of identical species which eat only one certain type of food.

Specimens born in captivity over-wintered better than wild-caught individuals, as is indicated below.

Published records on the breeding habits of *Natrix kirtlandii* are few in number. Hay (1893, 391) mentioned finding "three eggs in each ovary" of a specimen from Irvington, Indiana (USNM 17957). Each was a little less than $\frac{1}{2}$ inch in length. Another specimen from Winchester, Indiana (USNM 17953), contained eight eggs, each $\frac{7}{16}$ of an inch long. The two parent snakes, measured recently (after many years' preservation) are 375 and 361 mm. in length, respectively.

Atkinson (1901, 150) recorded the finding of "six partially developed embryos" in a female 14 inches in length, collected at Coraopolis, Pennsylvania, and Surface (1906, 140) found the same number of embryos in a specimen 15 inches long from West Sunbury, Pennsylvania. The embryos in the latter case were $4\frac{1}{2}$ inches long.

Additional information on reproduction in this snake, secured during the examination of preserved specimens, may be summarized as follows:

ANSP 5921, reputedly from Delaware County, Pennsylvania, 431 mm. in length, contains eight well-formed embryos; FMNH 2975, from Chicago Ridge, Illinois, 500 mm., twelve embryos; FMNH 16127, Evanston, Illinois, 463 mm., thirteen embryos; ISNHS 1361, Urbana, Illinois, 471 mm., contains two full-term embryos measuring 121 and 158 mm., respectively. No collecting date or data are given and it is not known whether this snake gave birth to other young before being killed. Two litters were born at the University of Michigan in 1919, one of seven individuals on August 30 and one of eight on September 5. Several of the young were preserved (UMMZ 58609).

Six litters of young born in captivity in the Toledo Zoo were reported in the "Reptiles of Ohio," p. 77. Since then two additional females in my possession have given birth to young, William Gessing, of Cincinnati, has supplied me with data on four more litters, and Paul L. Swanson, of Polk, Pennsylvania, has furnished information on another. These thirteen broods of young are summarized in Table 1. All of the three females from Cincinnati, collected on August 9, 1937, were found under the same rock. They were confined together and the young of the several litters were not separated.

The number of young in a litter (including published records and the evidence obtained from preserved specimens) may vary from 4 to 13. The mean is 7.81. These figures do not include the two embryos found in the female from Urbana since it is not known whether or not they would have constituted the entire litter.

Data on the lengths of young (91 specimens) are: Extreme range 127 mm. to 168 mm., interquartile range 142.1 to 155.4, mean 148.71 ± 1.03 , coefficient of variation 6.63 per cent. Newly born young averaged 1.39 grams in weight. In general, the larger females bore the largest number of young, but there were numerous exceptions to this statement. Dates of birth ranged from August 4 to September 24. In each case the parent snake stopped feeding two or three weeks before parturition.

The young were active as soon as they were born, many of them flattening their bodies and displaying the erratic movements characteristic of older specimens. All shed their skins within 36 hours of birth.

An attempt was made to raise two litters of young. The first of these (No. 5 in Table 1) was born August 24, 1933, to a female measuring 452 mm. in length and weighing 20.3 g. (measurements and weights made after bearing young). Two of the young died shortly after birth, the others ranged from 156 to 167, average 160.6 mm., in length, and from 1.3 to 1.4, average 1.3 g., in weight. On December 19, 1933, they averaged 164 mm. in length and 1.38 g. in weight. No attempt was made to mark these snakes in order to keep track of individuals, but it was obvious that at least two had lost weight. These weighed 1.1 g. each, less than the minimum at birth. This was in spite of the fact that all had accepted some food. All died before January 1, 1934.

Better success was achieved with the second litter. This (No. 6 in Table 1) was born September 8, 1933, to a female measuring 473 mm. and weighing 28.2 g. (after birth). The young were weighed and measured at intervals, with the following results:

Date Weighed and Measured	No. of Snakes	Lengths		Weights	
		Extremes	Average	Extremes	Average
Sept. 8, 1933	11	155-168	162.09	1.4-1.7	1.57
Sept 19, 1933	11	160-180	170.91	1.2-2.1	1.67
April 5, 1934	11	190-231	211.27	2.3-4.0	3.03
June 13, 1934	9	195-235	217.22	2.0-3.8	2.97
May 2, 1935	3	252-270	261.00	4.2-5.9	5.13

This group as a whole began to decline during the summer following birth. The young died one after another until only three remained. These three, however, appeared to be in perfect health, and possibly they might have attained their full growth in time had it not become impossible to observe them further.

Both litters were kept at ordinary room temperature the year round. The young ate earthworms exclusively, seizing these avidly, frequently engulfing worms as large as themselves, and tussling with their cage mates at feeding time. During their first year of captivity the eleven young snakes of the second litter shed (collectively) 53 times, or an average of 4.8 times each. These figures do not include post-natal shedding.

Owing to the fact that no considerable series of *kirtlandii* was collected in a single month or less, it has been impossible to make studies upon age groups and general rate of growth in the wild.

TABLE 1.—Birth of Young *Natrix kirtlandii*

No.	Date of Birth	Date Collected	Locality	Length of ♀	No. of Young	Size Range
1.	8/10/30	June, 1930	Toledo, O.	446 mm.	5	127-133 mm.
2.	8/4/31	May, 1931	Toledo, O.	394	8	146-156
3.	8/4/31	May, 1931	Toledo, O.	373	7	140-149
4.	8/15/31	8/12/31	near Hillsboro, O.	328*	7	127-145
5.	8/24/33	8/7/33	Toledo, O.	452	11	156-167
6.	9/8/33	7/6/33	Toledo, O.	473	11	155-168
7.	9/18-24/34	8/13/34	Forestville, Pa.	378*	4	132-142
8.	8/28/37	8/9/37	Cincinnati, O.	365	22	131-157
9.	8/28/37	8/9/37	Cincinnati, O.	445		
10.	9/5/37	8/9/37	Cincinnati, O.	405*		
11.	8/28/40	7/7/40	Cincinnati, O.	419*	7	150-162
12.	9/7/41	6/15/41	Wilkinsburg, Pa.	469	9	145-151
13.	9/21/41	6/15/41	Toledo, O.	452	7	146-151

* Part of tail missing.

Relationships

Until recently the relationships of *Natrix kirtlandii* with the other members of the genus *Natrix* have not been clear. Its unique position as the smallest and most terrestrial North American water snake, plus its secretive habits and utilization of slugs and earthworms as food, have set it apart from the larger and more active species. The recent discovery of *Natrix harteri* (Trapido, 1941), however, has supplied a clue which makes it possible to show that *kirtlandii* shares certain characteristics with at least one other species, and indicates that its affinities lie with the largest and most widespread group of American water snakes—*Natrix sipedon*, its subspecies and related species.

Natrix kirtlandii and *N. harteri* are similar in several respects. Basically their patterns are much alike. Dorsally, each is marked with four rows of blotches, the blotches being solid and averaging 50 or more in number from the head to a point above the anus. No other North American *Natrix* has so many dorsal markings of this type. Ventrally, the ground color of both *harteri*

and *kirtlandii* is orange or reddish and there is a dark spot or clouded area toward the lateral end of each ventral and subcaudal scute. In these characteristics *kirtlandii* shows a greater resemblance to *harteri* than it does to any other species.

Recently I have presented evidence (1942) to indicate that *harteri* is a member of the *sipedon* group of *Natrix*. It can also be shown that *kirtlandii*, in all probability, is a degenerate member of the same group and allied to it through a common ancestor of both *kirtlandii* and *harteri* which no longer exists.

Assuming that this premise be true, then it might be expected that *kirtlandii* would show reduction in scutellation, a phenomenon often associated with species having burrowing or secretive habits. This is exactly the case. When *kirtlandii* is compared with the *sipedon* group as a whole, marked reduction is evident in the number of scale rows, ventrals, subcaudals, labials, postoculars, and posterior temporals. The maximum number of scale rows is only 19, in comparison with 23 in *harteri*, *compressicauda*, and *clarkii*, and 25 or more in the others. The number of ventrals in *kirtlandii* varies from 121 to 136; only *pictiventris* and *compressicauda* have minima of less than 125 and these two also are the only forms which have maxima not equalling or exceeding the 136 of *kirtlandii*.* Subcaudals in males of *kirtlandii* vary from 57 to 69, and in females from 44 to 61. No member of the *sipedon* group has so few subcaudals in either sex as the minima for *kirtlandii*; the maxima for all considerably exceed the maxima for *kirtlandii*. The normal number of upper labials in *kirtlandii* is 6; in all the others it is 8. The normal number of lower labials in *kirtlandii* is 7; in all the others it is 10. Usually there are 2 postoculars and 2 posterior temporals in *kirtlandii*; in all the others there usually are 3 of each. There is also marked reduction in the relative size of the head and in general dimensions.

The number of teeth in *kirtlandii* also is reduced. The maxillary teeth in this species vary in number from 19 to 21; in the other members of the *sipedon* group they vary from 21 to 26. The number of pterygoid teeth in *kirtlandii* varies from 16 to 21; in the others it varies from 22 to 29. The number of mandibular and palatine teeth in *kirtlandii* falls within the range of variation as found in the other forms.

All of the above evidence indicates that *kirtlandii* is allied to the *sipedon* group. The possibility that its affiliations might be with some of the other New World *Natrix* has not been overlooked, however. With each of the others *kirtlandii* is at variance in one or more major considerations. The members of the *septemvittata* group—*septemvittata*, *rigida*, and *grahamii*—bear a striped pattern, they are somewhat attenuated in form and they have belly markings quite unlike *kirtlandii*. In *erythrogaster* and *transversa* the head is large, the eye is prominent, and there is a change in coloration and pattern associated

* The maximum number of ventrals in *pictiventris* and *compressicauda* may be shown to exceed this number when more material has been studied. Counts on which the various comparisons are based are from Clay (1936) and from my own data.

with age. The very large water snakes, *taxispilota*, *cyclopion*, *rhombifera*, and their related subspecies, are entirely unlike *kirtlandii* in such characteristics as basic patterns and number of scale rows. From *valida*, *kirtlandii* differs in pattern and in scutellation. The affinities of *valida* are not clear and this species is much in need of study.

In many respects, especially in habits and its relationships to other snakes, *Natrix kirtlandii* is comparable to *Thamnophis butleri* and *Tropidoclonion lineatum* (*Thamnophis lineatus* of Dunn [1932] and other authors). It may be said to occupy a position in relation to *Natrix* which is analogous to that occupied by *butleri* and *lineatum* in relation to the genus *Thamnophis*. These three snakes have much in common and each is the small, degenerate representative of a natural group—*butleri* of the *radix* group of *Thamnophis*, as defined by Ruthven (1908); *lineatum* of the *elegans* (*ordinoides*) group of the same genus, as suggested by Dunn, *op. cit.*; and *kirtlandii* of the *sipedon* group of *Natrix*. Each shows its closest affinities with a related form occurring chiefly or entirely to the west of its own range.

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* Letters in parentheses are those used to designate the various collections in the accompanying list of locality records. Not included above are ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum of Natural History; CU, Cornell University Museum; ISNHS, Illinois State Natural History Survey; SHS, Sandusky High School, Sandusky, Ohio; TMS, Toledo Museum of Science.

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Field Notes on Some Arizona Reptiles and Amphibians

Carl F. Kauffeld

The forty species of reptiles and amphibians contained in this report are represented by 101 specimens collected in Arizona in the Huachuca Mountains, the Chiricahua Mountains, the Douglas-Cochise region, Cochise County, and in the Tucson region in Pima County during sixteen days, from July 8th to 23rd, 1941. Besides observations on most of the habitats in which the specimens were collected, there are observations on the feeding, breeding, and behavior of many of them in captivity especially of some of the rarer rattlesnakes.

The collection was made primarily for exhibition at the Staten Island Zoo so that the bulk of the material was brought back to New York alive. Happily, in no instance has the locality datum on any specimen been lost or become confused. Specimens found killed along highways were preserved together with those unsuitable for exhibition. These, with those which were exhibited in the Staten Island Zoo collection and carefully preserved as they died, have been deposited in the herpetological collections of the American Museum of Natural History. Specimens found dead on highways will be referred to herein as "D.O.R." (dead on road) as is customary. Temperatures are in degrees Fahrenheit.

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AMPHIBIANS

Scaphiopus couchii Baird

Four specimens of this species were collected at night on the Sells-Robles road, in creosote-salt bush association, 29 miles west of U.S. Route 89, south-west of Tucson. Many others were observed in the same area.

Scaphiopus hammondii Baird

Two specimens were taken from a chorus of males calling from a roadside ditch 26 miles south of Cochise on U.S. Route 666. Large choruses of this species, together with *Bufo cognatus* in the same ditches, were encountered at frequent intervals between this point and Douglas. The region is essentially one of desert grass and mesquite, but at Douglas there is extensive irrigation. Ten days before our visit the ditches were dry, as the rains had not yet come, and not a frog was to be heard.

Bufo alvarius Girard

By July 11th there had been sufficient rain in the Tucson region to bring these toads out in numbers. Two specimens were collected at 9 P.M. in a water pocket in the rocks at 3100 feet in Bear Canyon, in the Santa Catalina foothills northeast of Tucson, in the sotol-cholla-sahuaro-ocotillo-palo verde association. The temperature at the time was 90°. These toads were numerous everywhere along roads and highways at night. On the night of July 13th a chorus of giant toads was heard from a ditch near the Sells-Robles road, southwest of Tucson.

Bufo alvarius is reported by dog owners in Tucson, whose pets cannot resist seizing the toads in their mouths, to represent a considerable danger to them. Musgrave (1930) reports fatal results to a terrier in two or three minutes. A Tucson veterinarian reports such fatal cases as frequent. Possibly nembutal could be used effectively in treating dogs stricken by *alvarius* poison as it has been against that of *Bufo marinus* (Turbot, C. R. 1938. Austral. Vet. Journ. vol. 14:152).

In captivity, our specimens could not be induced to take anything but grasshoppers, even refusing mealworms, a favorite food of the *Bufo marinus* that shared their cage.

Bufo cognatus Say

Two females were collected at night hopping on the road, U.S. Route 666, 9 miles south of Cochise. A few others were seen at various points through this desert grass region, but ten days later, after the rains had begun, the roadside ditches were occupied by huge choruses, probably numbering hundreds of toads and mating pairs, at several stations from a point about 26 miles south of Cochise to Douglas. *Scaphiopus hammondi* was associated with these toads in every chorus.

Bufo insidiosus Girard

One specimen was collected in a roadside ditch with *Bufo cognatus* and *Scaphiopus hammondi*, 30 miles south of Cochise. We could not be sure that the call of this species was distinguishable above the din of the other bufos and the undertones of the spadefoot. This was the only specimen we saw.

Bufo insidiosus (under the name *debilis*) has been reported once before from Arizona by Campbell (1934) from Miller Canyon in the Huachuca Mountains.

Bufo punctatus Baird and Girard

One specimen was taken at night in Bear Canyon, Santa Catalina foothills, northeast of Tucson, at approximately 3100 feet elevation. Another was found hopping with the sure-footedness of a *Hyla* on the steep side of a boulder in Cochise Stronghold one night at dusk.

Bufo woodhousii Girard

One specimen was found in lower Carr Canyon, Huachuca Mountains.

Hyla arenicolor Cope

Nine specimens of this *Hyla* from Bear Canyon range from very young to fully adult. They were found about an hour after dusk.

Rana pipiens Schreber

Like *Hyla arenicolor*, ten specimens of this species show considerable age difference. They were found in Bear Canyon at the same time as the *Hyla*.

TURTLES

Kinosternon sonoriense Le Conte

Two were found crawling on the road, U.S. Route 80 at St. David, Cochise County, at 7 A.M. They had evidently crawled from the irrigation ditches which paralleled the road at this point. Others were seen D.O.R.

These turtles seem to be more easily provoked into using their scent glands than other musk and mud turtles with which the writer has had experience.

Terrapene ornata Agassiz

Several of these turtles were observed on the road after 5 P.M. south of Cochise on U.S. Route 666. Only two were taken.

Gopherus agassizii Cooper

One specimen, presented by Mr. Snedigar, was found on a ridge 14 miles east of Tucson. When first seen it was busily eating sahuaro fruits.

LIZARDS

Coleonyx variegatus Baird

Three specimens were taken between 10 P.M. and 12 midnight at 11, 23, and 27 miles west of U.S. Route 89 on the Sells-Robles road, southwest of Tucson. The temperature at the time was 88° and there were occasional light showers. A bright light directed in their eyes caused these lizards to "freeze" like frogs at night in the light of a flash-light.

These lizards invariably eat their cast skins. The skin loosens in large patches and is seized in the mouth and swallowed as it comes away from the body. They carefully clean the old skin from each foot and digit, sometimes giving the appearance of removing a pair of tight gloves by seizing the tips of the fingers between the teeth.

A specimen from southern California thrived for over a year on a diet of mealworms, but its career in captivity was cut short by a *Gerrhonotus multicarinatus scincicauda* Skilton, which inadvertently gained access to the cage and ate the gecko.

There is apparently considerable difference in the inclination to display their vocal powers among specimens of *Coleonyx*. Some give voice very readily, others can be induced to do so only with difficulty or not at all.

Uta ornata linearis Baird

Only two of these lizards were seen and collected. They were a pair taken on an oak tree, the same tree but on consecutive days, in lower Carr Canyon, Huachuca Mountains, at about 5200 feet elevation.

Sceloporus clarkii clarkii Baird and Girard

A large gravid female of this species was taken in Carr Canyon on the same oak tree as the *Uta* mentioned above. This specimen, the only one seen, died August 6th. She carried 24 eggs, which contained embryos 4.5 to 5 mm. in length with eye spots and limb buds. Except for the fact that the eggs were covered by a well-developed shell, the late date to which the eggs were retained and the advanced state of the embryos, might suggest ovoviviparity in this species. Perhaps the incubation period is shorter than in most oviparous *Sceloporus*.

Sceloporus jarrovi jarrovi Cope

These lizards are extremely numerous everywhere in both the Huachuca and Chiricahua Mountains, especially around boulders over which they scramble with the greatest agility. Specimens were taken in Carr and Ramsey Canyons in the Huachuclas. As Gloyd (1937) points out, they are not in evidence below 5000 feet elevation although we saw some at 4800 feet in the Dragoon Mountains.

Undoubtedly this species figures largely in the diet of some of the rattlesnakes occurring at higher altitudes as well as other mountain snakes. Gloyd found scales of *S. jarrovi* in feces of *Crotalus triseriatus pricei*, and Campbell (1934) found these lizards in the stomachs of *Crotalus lepidus klauberi*. Both these snakes in captivity readily accept *Sceloporus*.

Sceloporus scalaris slevini Smith

One specimen was found sunning on a boulder, after a heavy rain, at about 8600 feet at Barfoot, Buena Vista Peak, Chiricahua Mountains. *Crotalus triseriatus pricei*, probably an important enemy of this lizard, was found close by.

Phrynosoma cornutum Harlan

One large gravid female was collected 22 miles north of Douglas, Cochise County, on U.S. Route 666, at about sundown. The eggs were laid on the sand of the floor of the collecting tin and remained unnoticed until after they had been crushed.

Phrynosoma orbiculare hernandesi Girard

Two specimens were found at about 8000 feet elevation on Carr Peak, Huachuca Mountains, and another one mile south of Paradise at 5400 feet in the Chiricahua Mountains.

Phrynosoma solare Gray

One specimen given to us by Mr. Snedigar was collected at Adams and Wilson Streets, Tucson. One observed northeast of Tucson about dusk escaped into a pile of detritus at the edge of a wash.

Heloderma suspectum Cope

Two specimens, a male and a female, were found together at 9:30 P.M., in a clump of vegetation in the dry, rocky stream bed of Bear Canyon, northeast of Tucson, at 3100 feet altitude. The temperature at the time was 90°.

Both lizards were active, their presence being disclosed by the rustling sound of their movement, but no courtship activity was noticed.

The Gila monsters' fondness for water, remarked on by Van Denburgh (1922), Ortenburger and Ortenburger (1926), and others, is strong. In captivity they spend as much time lying in their water pools as out of them, possibly more, yet remain in excellent health and thrive for years. That they will not thrive without water has been shown. Former reptile keeper Robert Hess, of the Philadelphia Zoo, states that in his many years experience he had little difficulty in keeping these lizards in good health so long as they were given access to water; deprived of it they languish and die. The same is true of *Heloderma horridum*. In a natural state they probably choose the vicinity of water. Although the stream bed was dry, for the most part, where the above specimens were collected, there were, nevertheless, well-filled water pockets in the rocks. Where no surface water is available, these lizards may employ their powerful digging ability to reach moisture below the surface.

The feces of these two specimens showed no identifiable remains. Ortenburger reports their feeding on other lizards, but certainly in captivity no other food than eggs is accepted. Other lizards, however small, placed in the same cage remain unmolested except for occasionally being crushed accidentally by the clumsy *Heloderma*.

The habit of frequently resting and sleeping turned over on their backs is remarkable. This is only an occasional practice with *Heloderma suspectum*; a specimen of *H. horridum* in the Staten Island Zoo almost always sleeps with the ventral side turned up and legs spread wide apart.

Cnemidophorus sexlineatus perplexus Baird and Girard

One specimen was surprised under a stone in Madera Canyon, Santa Rita Mountains, Santa Cruz County. Others were seen in Carr Canyon, Huachuca Mountains. These lizards are common in Boothill Cemetery, at Tombstone, but when abroad and active are difficult to catch by hand.

SNAKES

Heterodon nasicus kennerlyi Kennicott

Ono specimen, D.O.R., 22 miles west of Bisbee, Cochise County.

Coluber flagellum piceus Cope

An exceedingly red individual was collected by Logan Bostian at the junction of the road into Carr Canyon and Arizona Route 92. This snake fed readily on mice and lived amicably in the same cage with several specimens of *Alsophis angulifer*.

Coluber bilineatus Jan

One specimen from Carr Canyon Ranch, and another D.O.R. below the Ranch, represent this handsome species. The living specimen fed readily on mice and lizards.

Salvadora hexalepis deserticola Schmidt

A specimen that had apparently crawled out of one of the stone piles at the edge of the road into Ramsey Canyon, Huachuca Mountains, was found killed and badly crushed.

Phyllorhynchus browni browni Stejneger

Two D.O.R. specimens of this snake were found in the Tucson region: one east of Bear Canyon, Santa Catalina foothills, and another 9 miles west of U.S. Route 89 on the Sells-Robles road. Both were found at night. The second was killed between the time we passed this point at 10:30 P.M. and our return shortly after midnight. The temperature at the time was about 85°.

This species might be included with the forms listed by Gloyd (1937) as characteristic of his South-Central Desert faunal area.

Arizona elegans subsp.

One specimen was found crawling just after dark, 25 miles south of Cochise on U.S. Route 666. It is a male measuring 700 mm., the tail .155 of the total length; ventrals, 198; subcaudals, 54; scale rows at midbody, 27. Very dark in color, the dorsal body blotches number only 49, although they are very narrow. This specimen approaches *elegans*, yet the number of scale rows and the narrow body blotches are like *occidentalis*.

Pituophis sayi affinis Hallowell

Seven specimens were collected: three on U.S. Route 666 between Douglas and Cochise; one at Dragoon, Cochise County; one 2 miles north of Paradise, Chiricahua Mountains, at 5200 feet; one 6 miles west of U.S. Route 89 on the Sells-Robles road, Pima County; and one at the Country Club Road and East Speedway, Tucson. All were found abroad and active from five o'clock in the afternoon until after midnight. One was found at 8:30 in the morning. Most individuals are gentle from the moment of capture, but hiss loudly, strike and actually bite.

Lampropeltis getulus splendida Baird and Girard

One specimen was found just before sundown on U.S. Route 666, 18 miles north of Douglas. Another was seen D.O.R. at Cochise, but was too crushed to preserve. Mr. Logan Bostian collected a juvenile specimen late in July between Douglas and Cochise. Apparently this species favors the neighborhood of irrigation ditches, a predilection for moisture shared with most of the *getulus* group.

In scale characters both specimens are within the range of variation defined by Blanchard (1921); both are males; the adult measures 1090 mm. in total length, the juvenile, 520 mm.

The pattern of the juvenile (Fig. 1) is sufficiently different from that of adults to warrant description. The head pattern is like that of the adult, the dark brown coloration extending almost a full head length onto the nape, uninterrupted except for two small light occipital spots. In the dorsal pattern

of distinct dark blotches each blotch is solidly colored except for occasional light centered scales at the edges. The blotches are separated all around by one or two scale lengths of white ground color with a very faint dark outline visible on each light scale. This dark outline widens with age, finally enclosing a small light area in each scale, thus producing the speckled appearance so characteristic of the adult. There is a clearly defined series of alternating lateral blotches, only occasionally in contact with the dorsal blotches. These are formed entirely of light centered scales except posteriorly where they become solid and confluent with the dorsal series, but for the most part all the blotches are well separated and the ground color extends uninterrupted to the ventrals. The lateral blotches are confluent with the dark areas of the venter.

The adult specimen has no light colored scales anywhere, dorsally or laterally, but the middorsal pattern of solid dark blotches is quite distinct, and the alternate lateral series is fairly discernible only because the scales of these blotches have smaller light centers than those surrounding them. With its well

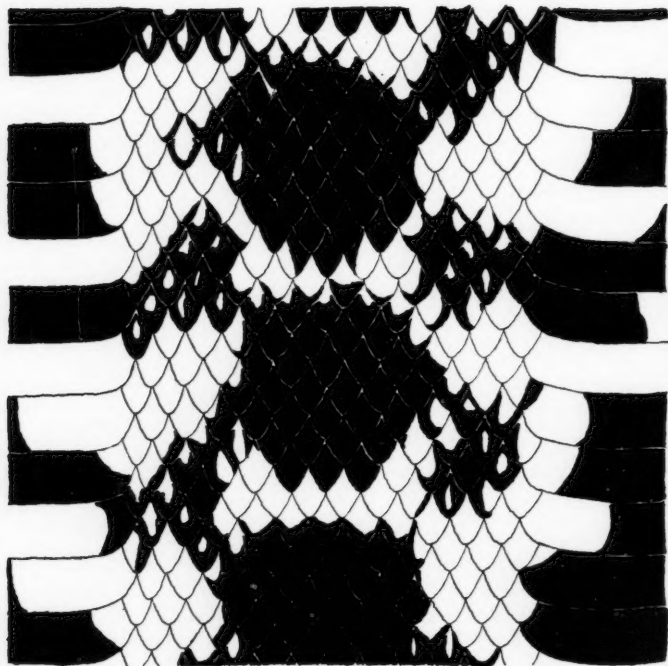


Fig. 1. Juvenile pattern of *Lampropeltis getulus splendida*.

defined markings and large areas of solid color, the juvenile pattern is essentially more like that of typical *getulus* than any other of the speckled races, and certainly more so than the banded, such as *yumensis* and *boylii*. The young of *Lampropeltis getulus holbrooki*, which might be expected to show more solid areas of color, are speckled to the same degree as the adults.

Thamnophis eques cyrtopsis Kennicott

Two very small young were observed in a shallow water pocket in Bear Canyon, Santa Catalina foothills, at about 9 P.M. One adult specimen was found on a road northeast of Tucson near Bear Canyon on the same night.

Thamnophis marcianus Baird and Girard

An adult of this species was found on the same road on the same night as the adult example of the preceding species. This specimen fed readily on pieces of chopped fish and earthworms. Marcy's garter snakes will also take lizards and mice.

Hypsiglena torquata ochrorhyncha Cope

Two specimens were found on the Sells-Robles road, 24 miles and 29 miles west of U.S. Route 89, southwest of Tucson, between 11 P.M. and midnight. One of these snakes was found swallowing a *Scaphiopus couchii* of medium size which had been crushed by a car. Not even being picked up and placed in a bag distracted the snake from its meal, and later examination showed ingestion had been completed.

Another large adult was found at Carr Canyon, Huachuca Mountains.

Crotalus cerastes Hallowell

One specimen was found at an elevation of 2550 feet at the eastern periphery of the range of this species, 8 miles east of Red Rock in Piñal County. The temperature at the time (9:45 P.M.) was 85°.

A resident of Red Rock told us that sidewinders are very common in the region and that dogs are frequently bitten, but invariably recover. Mr. Arrington has had a collector find them in considerable numbers near Maraña, a short distance southeast of Red Rock.

These specimens are much darker in color than those I have seen from the Colorado desert of California, an apparent correlation with the color of the soil. Gloyd (1937) remarks on this difference between examples from Ajo, where the soil is dark, and those from Yuma, where it is light. Colorado Desert sidewinders are lighter at all times, even when freshly caught, than our central Arizona specimens. Klauber (1931) indicates that these differences are effected by individuals, and that they are comparable to the color changes in certain lizards though less marked. He includes *Crotalus viridis oreganus* with *C. cerastes* in having this power. In my experience, many snakes become lighter in color in captivity, after several skin molts. This is particularly noticeable in *C. v. viridis*, of which I have had hundreds under observation, and also of *C. v. oreganus*, but always as a gradual change from dark to light,

quite unlike the color changes in lizards such as *Sceloporus* and *Anolis*. Storey and Wilson (1932) remark on the lightening of color in their captive *C. v. oregonus*. Rahn (1941) produced changes from dark to light in *C. v. viridis* by hypophysectomy. Captivity may cause a physiological disturbance with similar effects.

Like most sidewinders, our Arizona specimen accepted lizards and mice with equal readiness.

Crotalus lepidus klauberi Gloyd

One specimen was found on the bare surface of a huge granite boulder on Carr Peak, Huachuca Mountains, at 6700 feet elevation, in shade, with the temperature at 90° at about 2 P.M. This was a female measuring 429 mm. which gave birth to four young on August 9th.

A second female measuring 422 mm. was taken in Ramsey Canyon in an open, rocky area at 6000 feet, 9:30 in the morning. These rocks support a growth of cacti, agaves and stunted pines, unlike the adjacent portions of the slope, which is covered by forest trees (Pl. 1-upper). Numerous crevices afford retreats for the snakes, which rattle and disappear into them at the approach of the collector. Mr. Bostian collected a fine male measuring 538 mm. at this same location later in July. Unlike the two females which had a blue-gray ground color, this specimen had a beautiful greenish tinge, almost iridescent in quality.

All three of these snakes fed readily upon *Sceloporus undulatus* in captivity, and on one occasion *Eumeces laticeps* was taken. Mice were refused, but accepted by at least one of the young. Falck (1940) lists mice, frogs, and even salamanders (*Ambystoma*) being taken by a specimen of typical *C. lepidus* from Texas. Campbell (1934) found the remains of *Sceloporus j. jarrovi* in the stomachs of two of three specimens taken at 6500 feet in Miller Canyon, Huachuca Mountains. Undoubtedly these lizards form the principal food supply of the species for they are ubiquitous in the habitat of *C. l. klauberi*. We found lizard remains in the feces of our specimens. Gloyd (1937) reports that captive specimens accept mice eagerly, but believes that individuals of *Sceloporus j. jarrovi* "form a considerable part of the food of this species."

In disposition *C. l. klauberi* is timid but quite irritable, frenzied at times, a quality of temperament exhibited by adults and young alike. Although the degree of irritability varies with individuals, all were more easily disturbed (as shown by rattling at the slightest provocation), than specimens of our seven other species of *Crotalus*. Nor did the specimens become more calm when finally established in cages in the Zoo.

Crotalus molossus molossus Baird and Girard

One adult male was found lying in deep shade on a ledge at the opening of a crevice in granite boulders near a stream on Carr Peak, Huachuca Mountains, at 6700 feet elevation, at about 11 A.M., only a few yards from the spot where *Crotalus lepidus klauberi* was taken. The rock ledges, surrounding forest,

and leaf-filled crevices suggest strongly the rocky retreats of *Crotalus horridus* to which *molossus* bears some similarity in general appearance. Another male specimen was found nearby but somewhat below the level of the road to the Reef Mine on Carr Peak. The first specimen accepted dead mice readily, but refused lizards. It died within three months of a bacillary infection of the lungs. A female that gave birth to six young was collected in Ramsey Canyon, Huachuca Mountains, by Mr. Jack Breed, July, 1937. Mrs. Healy reports seeing a specimen abroad in Carr Canyon region late in November with a thin covering of snow on the ground.

The climbing of *Crotalus molossus* was mentioned by Cope (1900) who reports a specimen as "in the act of springing through a bush." Col. M. L. Crimmins writes in a letter, "I kept some in bird cages and at night they would climb up on the limbs of branches. I examined one after it was killed about 25 miles northwest of San Antonio (Texas) in a tree about nine feet above the ground with no limb closer than five feet." Texas specimens received at Staten Island Zoo immediately accepted a tree placed in their cage as a resting place and the Arizona specimens likewise showed a slight inclination to coil in branches just above the ground.

The sound produced by the large rattle of this species has a strident quality that is startling and quite unlike other rattlesnakes of my experience. Most specimens are quiet and docile, but occasionally the maneuvers of a keeper will exhaust the snake's patience and cause the sharp warning to be sounded.

Crotalus scutulatus scutulatus Kennicott

We encountered these snakes only on roads while driving at night. One specimen was found 7 miles south of Cochise on U.S. Route 666 at 8:45 P.M. Mr. Bostian collected three others on this road between Cochise and Douglas later in July. A young specimen was found on the Sells-Robles road, southeast of Tucson, 14 miles west of U.S. Route 89, at about 10:30 P.M. Another D.O.R. on the same road one mile west of U.S. Route 89 contained the remains of a large *Cnemidophorus* (probably *perplexus*). Other D.O.R. records are one north of Douglas and one 13 miles west of Lowell in Cochise County, another south of Oracle Junction, Pima County, and one west of Las Cruces, New Mexico.

Crotalus scutulatus scutulatus is a quiet snake in captivity and feeds readily on white mice. All our specimens, except the young example from Pima County, soon died. Many apparently unharmed snakes found on roads presumably succumb to little noticeable injuries received from glancing blows of passing auto wheels.

Crotalus tigris Kennicott

We failed to find this species, but were given a specimen by Mr. O. N. Arrington collected in June at Santa Catalina Foothills Estates, north of Tucson, in the sahuaro-palo verde-ocotillo association. This snake was very quiet in disposition and accepted lizards readily. It is unquestionably another



PLATE 1. (Upper) Habitat of *Crotalus lepidus klauberi*, Ramsey Canyon, Huachuca Mountains, at 6,500 feet elevation. Exposed, exfoliating rocks support a growth of cacti and agaves. (Lower) Habitat of *Crotalus triseriatus pricei*, Barfoot, Chiricahua Mountains, at 8,800 feet elevation. Numerous crevices in the lichen covered rocks afford convenient retreats for this species.

of the lizard-eating rattlesnakes. Ortenburger and Ortenburger (1926) found a specimen with the tail of a lizard just disappearing down its throat.

Crotalus triseriatus pricei Van Denburgh

Three adult specimens were secured between 8500-8800 feet at Barfoot, Buena Vista Peak, Chiricahua Mountains (Pl. 1-lower). All were found within a small area of exposed boulders at about 1 P.M., sunning after the cold downpours that had been in progress since the previous evening. The temperature had dropped to 56° at 11 A.M., but with an hour of sunlight the rise in temperature was sufficient to bring the snakes out of their retreats. The three were taken within an hour, after which clouds once more obscured the sun and the temperature dropped from 75° to 61° at 2:45 P.M. Each of our specimens rattled briefly when surprised and attempted to escape into crevices in the lichen-covered rocks. The rattle is so feeble as scarcely to be heard. They did not resent capture and lay quietly without rattling when taken out of the collecting bag half an hour later. This calm behavior was in strong contrast to the nervousness of *C. l. klauberi*. Undoubtedly they are more numerous than is commonly supposed, but at high altitudes and in difficult terrain.

The largest of our specimens was a male measuring 514 mm. One measuring 455 mm., a gravid female, gave birth to six young on August 19th. All of our specimens accepted *Sceloporus* readily but refused mice. Lizard remains were distinguishable in the feces found in the collecting bags. Lizards were refused if alive but taken dead, as was true also of the green rock rattlesnakes. One of our Price's rattlers would take a lizard held out to it on a forceps.

Crotalus willardi Meek

Two fine specimens of this species were secured in Ramsey Canyon, Huachuca Mountains, at about 6800 feet. The day had begun overcast with clouds from storms of the night before still obscuring the sun, but by 11 A.M. the temperature was about 75° and there was strong sunlight, which had not yet heated the ground sufficiently to prevent activity of snakes. The larger of the two specimens, a male measuring 600 mm., was found basking on a rock in a stony glade, completely surrounded by dense forest, at a point below the site of the old Hamburg Mine between the trail and the nearby stream. The snake rattled briefly as I approached and disappeared rapidly under a rock. On turning the rock, a second specimen, a 460 mm. female, was found partly covered by the snake that had just entered the retreat. Although both resented capture fiercely, they ceased rattling immediately on being placed in a bag and thereafter were exceptionally quiet. Many more rocks were turned but no other snakes were found.

So little has been recorded concerning the habitat of *Crotalus willardi* that nine plants associated in this spot were collected at random. I am indebted to the specialists of the Bureau of Plant Industry, Division of Plant Exploration and Introduction of the United States Department of Agriculture, for the identification of the plants, which were: New Mexican locust (*Robinia neomexicana*), buckthorn (*Rhamnus crocea ilicifolia*), big-tooth maple (*Acer*

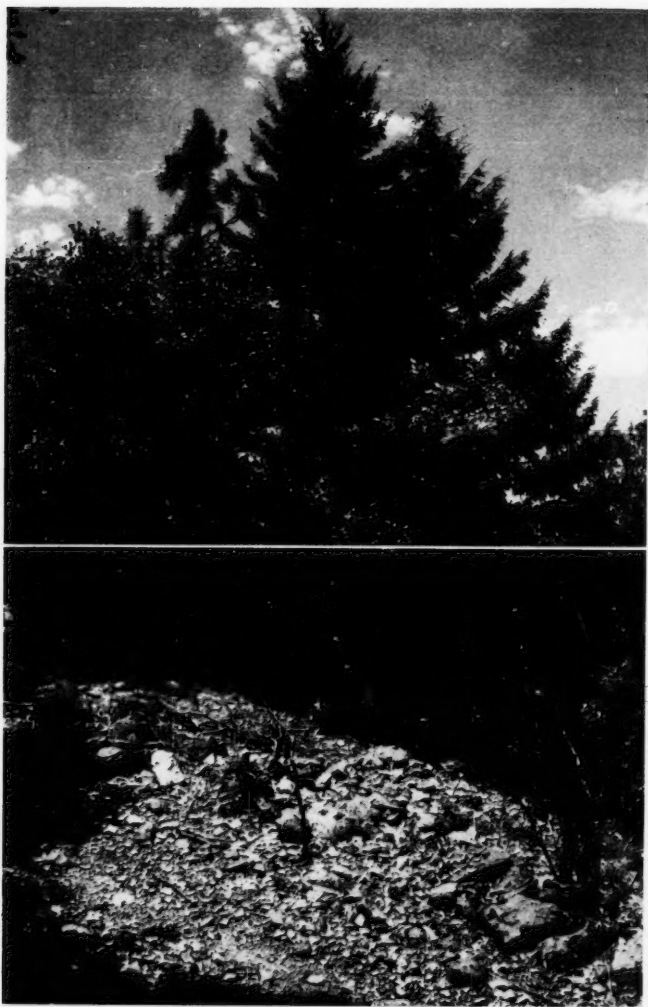


PLATE 2. Habitat of *Crotalus willardi*, Ramsey Canyon, Huachuca Mountains, at 6,800 feet elevation. Two specimens were found under the light colored rock left center. Note dense surrounding forest and tree-top view showing Douglas fir, limber pine and Arizona white oak. See page 353.

grandidentatum), ash (*Fraxinus velutina glabra*), Arizona white oak (*Quercus arizonica*), limber pine (*Pinus flexilis*), Douglas fir (*Pseudotsuga taxifolia*), white fir (*Abies concolor*), and red cedar (*Juniperus scopularum*). All these grew within a radius of twenty feet, and indicate the moist, heavily wooded nature of the *Crotalus willardi* habitat niche. This is in contrast to *Crotalus lepidus klauberi* which usually chooses dry bare prominences of canyon walls, with exposed and exfoliating rocks, supporting little growth other than cacti and agaves, but adjoining the forest areas. Although both may occur in the same general locality, *Crotalus willardi* is an alpine forest snake. Such a restricting factor would in part account for the highly localized distribution of the species in southeastern Arizona. This is another form to be included in Gloyd's "Eastern Mountains" faunal area, which is an extension northward of William H. Burt's "Apachian-Durango" provinces (Smith, 1939). The homology of these faunal areas is indicated by the distribution of *Crotalus triseriatus pricei*, *Sceloporus scalaris slevini*, *Sceloporus jarrovi jarrovi*, and possibly *Eumeces callicephalus*. *Crotalus willardi* may eventually be found in the Chiricahua Mountains.

The habits of *Crotalus willardi* are little known for there have been no observations made on living examples, other than those included here, so far as I know.

The most conspicuous difference in the two individuals under my care was in their activity. Although both showed a great deal of curiosity concerning movements in the neighborhood of their cage, the male was always more active and spent more time out of hiding. The female remained within the rock retreat with only the head occasionally showing to watch movements outside, whereas the male, when not crawling about, would lie extended or loosely coiled. These snakes less frequently assume the characteristic symmetrical resting coils of the rattlesnakes, with the neck in an S curve and the head resting on the body, but like colubrids, they usually have no characteristic posture. They resemble *Agkistrodon* and *Bothrops* in this and other respects.

After these two specimens were established in permanent quarters in the Zoo, they were offered white mice as food. The larger immediately struck a 20-gram mouse, which showed immediate symptoms of toxemia and was unable to move. Within a quarter of a minute it had rolled on its back with legs kicking convulsively, and in half a minute all struggles had ceased. In losing control of its limbs, the mouse rolled toward the smaller snake, which without hesitation seized it by the snout before its struggles had quite ceased, and began to engulf it. In order to prevent the larger from interfering with the smaller, a second mouse was quickly killed and laid before it. The snake hardly had time to notice the substitution. A very minute examination of the substituted mouse was begun, ending with a beginning of the laborious process of ingestion. After a few hesitant movements of the jaws, the head was drawn back and the jaws closed. After a half hour of roaming about the cage, the snake returned to the morsel, the deliberate and minute examination was again gone through but after another seizing of the snout, it was again rejected. This

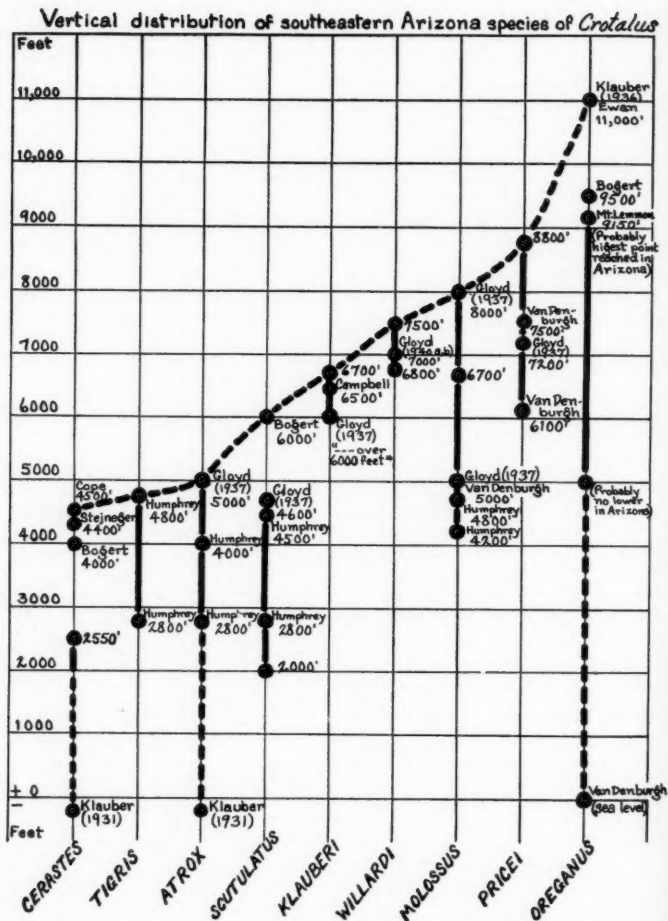


Fig. 2. Vertical distribution of species of *Crotalus* in southeastern Arizona. Solid vertical bars indicate the known limits of altitudinal range for the species in southeastern Arizona. Broken curve indicates known limits to which the species, or subspecies, ascends over its entire range. Broken vertical bars indicate limits to which the species descends in other parts of its range.

individual never fed voluntarily, but frequently displayed interest in food; it never seemed to be able to surmount some psychological hurdle in the way of actually taking it. White mice, fed forcibly, were assimilated. This was the only occasion on which either of these snakes could be induced to strike living prey, but this single observation suggests that *Crotalus willardi* has a venom of high toxicity.

The smaller snake fed eagerly on white mice offered dead, always refusing living food. Both snakes refused lizards (*Sceloporus*). Van Denburgh (1922) mentions that a specimen of *Crotalus willardi* found in the Santa Rita Mountains had a mouse in its stomach. Presumably this species does not compete with *C. lepidus klauberi* and *C. t. pricei* for lizard prey in the same region.

It is a little known fact that captive snakes frequently accept dead food when refusing living prey. This seems especially true of crotaline snakes. In fact, with a high percentage of all of our captive snakes, dead prey is preferred even if living animals are also accepted. This is not necessarily a matter of conditioning, for the writer has had recently caught specimens take dead prey without hesitation. The prudent reptile keeper will take advantage of this inclination to eliminate the confusion and disturbance incumbent on feeding many snakes in one cage. Danger from aggressive prey, such as rats, is eliminated; competition for or dispute over certain morsels is reduced. Many specimens lack sufficient courage or initiative to make a kill, but will attempt to take away another less timid cage mate's prey. Others always seem to prefer what another snake has to what lies immediately before them. Offering dead food obviates or reduces most of these difficulties.

The force-fed snake retained and digested eight adult mice normally during 107 days, and shed two perfect skins at intervals of 65 days, between July 20th and November 12th. The "opaque" period was of seven days duration in each instance between the time the first faint clouding of the eyes was observed until ecdysis was completed. The smaller specimen consumed six mice voluntarily in the course of one month, but refused food after September 3rd, yet remained in seemingly good health. The skin was sloughed only once in the same period, on August 31st. Both snakes drank water frequently.

Mr. Jack Breed of Swampscott, Massachusetts, kindly permits me to include in this account some observations on an 18 inch male specimen of *Crotalus willardi* found by him under a piece of tin near the site of the Hamburg Mine in Ramsey Canyon in July, 1937. The specimen is now number 43391 in the collection of the Museum of Comparative Zoology. He describes its behavior as "extremely vicious when first captured, usually turning and biting instead of striking as other members of the genus do. After several days in captivity, the specimen became surprisingly gentle, could not be induced to bite, and never rattled. We often handled the reptile which showed no signs of anger."

The peculiar behavior in turning to bite is decidedly foreign to the action of most rattlesnakes, but is common among species of *Agkistrodon* and *Bothrops*. He mentions that his specimen would bite a stick if touched with it.

This snake was kept alive for eight weeks during which it steadfastly refused lizards, toads, mice, "and other possible snake food." It did, however, show great fondness for water.

A further specimen has come into my possession, collected by Mrs. Healy during June, 1942, at the head of Carr Canyon at 7500 feet elevation. This snake is an adult male, exceptionally stout and light in coloration. It differs from the individuals mentioned above in being far more irritable and exceedingly timid, although it may remain out of hiding most of the day. Despite its irritability, it has never struck at a threatening object but shares with the others inquisitiveness concerning activity in its vicinity. If a finger is placed against the glass of its cage, the snake will immediately leave its resting place and quickly investigate by flicking the glass with its tongue. Moreover, it will follow the finger wherever it may be moved with quick bird-like motions. At first this was taken to indicate a desire for food, but although mice, lizards, frogs, and fish were offered, nothing has been accepted.

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STATEN ISLAND ZOOLOGICAL SOCIETY,
STATEN ISLAND, NEW YORK.

Amphibians and Reptiles of Tioga County, New York

Robert T. Clausen

Tioga, one of the southern tier of counties of New York, is located entirely in the Glaciated Allegheny Plateau and in the drainage of the Susquehanna River. North and south, the county ranges in length from 30 km. (18 mi.) to 45 km. (28 mi.) and in width from 10 km. (6 mi.) to 39 km. (24 mi.). Altitudes range from 232 m. (760 ft.) to 612 m. (2009 ft.).

The collecting of the herpetological fauna of the county seems to have begun about 90 years ago. DeKay (1842) mentions no definite collections, but a few years later, from 1853-62, A. Mayor and others were sending specimens of salamanders, frogs, snakes, and turtles to Professor Agassiz at Harvard. These specimens are preserved in the Museum of Comparative Zoology at Cambridge. Eckel and Paulmier (1902), however, do not cite specific records from the county.

Most active herpetological exploration in the area was in the period between 1930 and 1940. Several collectors from Cornell University made trips into the county and brought back specimens. Bishop (1941) has cited the records for salamanders, but additional collections have accumulated since his publication. These are recorded here, also the data concerning frogs and reptiles.

In the discussion under each species, extreme dates are given to indicate seasonal occurrence. There is also indication, in most cases, of the number of localities at which specimens have been seen.

Names of museums are abbreviated as: CU — Department of Zoology, Cornell University, Ithaca, New York; MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; US — United States National Museum, Washington, D. C.

Annotated List

Triturus viridescens viridescens (Raf.).—Adults common in shallow water of pools, ponds, and sluggish portions of streams; red eft frequent in woods. April 16, 1939, pool at headwaters of Dean Creek, Spencer Tp., R. T. C., to November 13, 1938, pond 2.5 km. east of Flemingville, R. T. C. and H. Trapido (CU). 14 localities.

Ambystoma maculatum (Shaw).—Only one record, a specimen in an old log near Miami Creek, about 5.5 km. north of Barton, Barton Tp., R. T. C., H. Trapido, and W. C. Wilson no. 3370 (CU).

Hemidactylum scutatum (Schlegel).—Rare, only one collection, an individual from under a flat stone on a wooded slope 1 km. southeast of Lockwood, November 6, 1938, R. T. C. & R. H. Wilson no. 3737 (CU).

Plethodon cinereus (Green).—Common and generally distributed under stones and logs in woods. The red-backed phase is much commoner than the lead-backed phase. Of 58 individuals noted in the field at 14 localities, only 4 (7%) were the lead-backed phase. April 16, 1939, Barton Tp., R. T. C., to November 13, 1938, .3 km. east of Flemingsville, R. T. C. and H. Trapido (CU). 17 localities.

Plethodon glutinosus (Green).—Scarce; under stones and logs in woods. Only 3 records. Wooded slope .8 km. southeast of Lockwood, November 6, 1938, R. T. C. & R. H. Wilson 3736 (CU); woods 2.5 km. south southwest of Glencairn, May 7, 1939, R. T. C. & R. H. Wilson (CU); ravine east northeast of Straits Corners, May 17, 1942, R. T. & E. R. C.

Gyrinophilus porphyriticus porphyriticus (Green).—Scarce; under stones in streams. Three records: 2 under flat stones in small stream tributary to Dean Brook, Barton Tp., April 16, 1939, R. T. C. & R. H. Wilson 3846 (CU); several specimens from Berkshire, Museum of Comparative Zoology at Cambridge; cited by Bishop (1941) from Richford and vicinity.

Eurycea bislineata bislineata (Green).—Frequent under stones in or along brooks. April 13, 1941, Candor, R. T. C., to November 13, 1938, small brook 2.5 km. east of Flemingsville, R. T. C. & H. Trapido (CU). 13 localities.

Eurycea longicauda (Green).—Scarce, under stones near streams. April 27, 1935, Candor, E. E. Brown et al. no. 2839 (CU), to October 14, 1935, Candor, A. H. Wright et al. no. 2926 (CU). Besides the locality along Catontk Creek at Candor, this species has also been found about 1.5 km. north of Candor, along Willseyville Creek at Willseyville, and in Cayuta Creek south of Van Etten. Also it is reported from along the Susquehanna River near Nichols and from near Waverly.

Desmognathus fuscus fuscus (Raf.).—Frequent under stones in brooks and about springy places. April 13, 1941, Candor, R. T. C., to November 6, 1938, Barton Township, R. T. C. 10 localities.

Desmognathus ochrophaeus ochrophaeus (Cope).—Scarce; under stones in and along brooks. Berkshire, A. Mayor (MCZ); ravine east northeast of Straits Corners, May 17, 1942, R. T. & E. R. C.; Willseyville, April 25, 1937, R. T. C. (CU); Glencairn, May 7, 1939, R. T. C. 3855 (CU).

Bufo americanus americanus Holbrook.—Common. Earliest record—April 21, 1931, 1 heard trilling south of Willseyville, R. T. C.

Hyla crucifer Wied.—Common, more often heard than seen. April 16, 1939, headwaters of Dean Creek and Brook at boundary of Barton and Spencer Townships, R. T. C. & R. H. Wilson, to November 13, 1938, 2 miles east of Flemingsville, Oswego Township, R. T. C. & H. Trapido.

Hyla versicolor versicolor (LeConte).—Probably frequent, but rarely observed. Heard calling from late May to the middle of July. Earliest record—May 27, 1939, several calling on slope south of Willseyville, R. T. C. Otherwise recorded only at Spencer and Willseyville.

Rana catesbiana Shaw.—Definite records from Candor; 2 miles north of Lockwood; and Butson Creek, Barton Township. Latest record—November 13, 1938, 1 under stone at edge of Cayuta Creek 2 miles north of Lockwood, R. T. C. (CU).

Rana clamitans Latreille.—Common in pools and streams. April 27, 1939—headwaters of Dean Creek, Spencer Township, R. T. C. & R. H. Wilson 3854 (CU), to November 2, 1935, Willseyville, H. Trapido & K. F. Lagler 3274 (CU).

Rana palustris LeConte.—Common about streams and pools. In the hills, commoner than *R. pipiens*. April 27, 1939, pool at headwaters of Dean Creek, Spencer Township, R. T. C. & R. H. Wilson 3853 (CU), to November 13, 1938, along small brook $1\frac{1}{2}$ miles east of Flemingsville, Owego Township, R. T. C. & H. Trapido (CU).

Rana pipiens Schreber.—Common about water and in meadows. In the valleys, more abundant than *R. palustris*. March 26, 1939, banks of small pools about one mile south of Candor, $10\pm$, R. T. C., to October 29, 1934, Candor, 1, W. J. Koster 2931 (CU).

Rana sylvatica LeConte.—Common in woods. April 16, 1939, Spencer Township, calling in chorus, R. T. C., to October 9, 1930, Willseyville, R. T. C.

Eumeces anthracinus (Baird).—Frequent in the drainage of Willseyville Creek. Many individuals have been caught or observed in Prospect Valley. First recorded from there on May 11, 1938, when five were found under flat stones on an overgrown pastured slope (alt. 365-425 m.) on west side of valley 1 km. north northeast of Perryville, R. T. C. and H. Trapido. Temperature was cool, slightly above freezing point, after a period of warmer weather. This condition of weather has been most satisfactory for obtaining specimens of *Eumeces*. The animals are under stones, rather lethargic, and easy to catch. In warmer weather, they are so active that observation or capture are both difficult. Most records are in the spring, late April or May, but there is at least one collection made as late as October (Oct. 8, 1938, A. H. Wright and *Herpetology Class*). Besides the slope on the west side of Prospect Valley and the corresponding slope on the west side of the ridge north of Willseyville, there is only one other locality where the beast has been taken—valley of Cata-tonk Creek about 2 km. north of Candor, April 27, 1938, Elmer Brown 2310 (CU).

Diadophis punctatus edwardsii (Merrem).—Probably frequent, but found at only four localities, under stones on hillsides. May 1, 1938, Candor, R. T. C., H. Trapido, and J. T. Baldwin, Jr., to October 25, 1931, Prospect Valley, R. T. C.

Opheodrys vernalis (Harlan).—Frequent in open woods, also in bog at Oakley Corners. Collected at Berkshire in 1862 by A. Mayor and sent to Professor Agassiz at Cambridge (MCZ). My records are in May and June, earliest May 11, 1938, Prospect Valley, R. T. C. and H. Trapido 2306 (CU).

Coluber constrictor constrictor (L.).—Only one record, a specimen collected at Nichols, R. Howell 7194 (US).

Lampropeltis triangulum triangulum (Lacépède).—Probably common, but collected only in Prospect Valley and at Candor. My earliest record is May 1, 1938, Candor, R. T. C., H. Trapido, and J. T. Baldwin, Jr., 2309 (CU).

Natrix sipedon sipedon (L.).—Common along streams. April 13, 1941, Candor, R. T. C., to October 25, 1931, Prospect Valley, R. T. C. & H. Rahn. The specimens found on the last date were going into hibernation in a rocky place on the slope on the west side of Prospect Valley.

Storeria dekayi (Holbrook).—Only two records, both reported by H. Trapido from east side of valley of Cayuta Creek between Lockwood and Van Etten in Chemung County. This species is definitely rarer in Tioga County than it is in the counties to the northwest.

Storeria occipito-maculata (Storer).—Common in open woods and overgrown fields. Usually found under stones, but occasionally seen in open, particularly late in season. April 17, 1938, South Apalachin, R. T. C., J. T. Baldwin, Jr., and W. C. Wilson 3402 (CU) to November 7, 1937, Prospect Valley, R. T. C. & H. Trapido 3265 (CU). Seven individuals were excavated from among stones on slope on west side of Prospect Valley on October 25, 1931. These were in association with *Natrix sipedon* 9, *Diadophis punctatus* 1, and *Thamnophis sirtalis* 1. Both brown and fuscous individuals occur.

Thamnophis sauritus sauritus (L.).—Three specimens: a ♀ from Summit Marsh, North Spencer, collected in June, 1933, gave birth to 11 young in laboratory August 6-7, J. W. Large 1631 (CU); Spencer Lake, August 1, 1937, R. T. C. 2191 (CU); and R. H. Howell 7222 (US), without definite locality.

Thamnophis sirtalis sirtalis (L.).—Abundant, April 16, 1939, Barton Township, R. T. C. & R. H. Wilson 3847 (CU) to November 4, 1934, Spencer Township, R. T. C., R. Smith, and W. T. Winne.

Chelydra serpentina (L.).—Probably not rare, but only 1 specimen preserved, Berkshire, A. Mayor (MCZ).

Clemmys insculpta (LeConte).—Three records; earliest, April 17, 1938, Waite Settlement, R. T. C. 3401 (CU); others from Prospect Valley and Oakley Corners.

Chryseis picta marginata (Agassiz).—Frequent about ponds, lakes, and streams, also in the wetter swamps. An individual with plastron immaculate was collected at Spencer Lake on August 1, 1937, R. T. C. 2731 (CU).

Summary

There are definite records for 31 species of amphibians and reptiles which are known to occur in Tioga County. *Hemidactylium scutatum*, *Plethodon glutinosus*, and *Ambystoma maculatum*, not reported from the county by

Bishop, all were to be expected. Species not recorded in the present list, but also to be expected, are *Cryptobranchus alleganiensis*, *Ambystoma jeffersonianum*, *Pseudotriton ruber*, *Elaphe obsoleta* and *Crotalus horridus*. Only 7% of the specimens of *Plethodon cinereus* observed were of the lead-backed phase. *Storeria occipito-maculata* and *Natrix sipedon* were observed going into hibernation on a rocky slope in Prospect Valley. *Eumeces anthracinus* is frequent in this same valley.

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Additional Notes on the Occurrence and Natural History of the Triple Tail, *Lobotes surinamensis*

J. L. Baughman

Kelley (1923) recorded the appearance of the Triple tail in some numbers. These data were added to by Gudger (1931), by Hughes (1937), and by Baughman (1941). The purpose of the present note is to add to the foregoing data, in condensed form, more material on the range and natural history of the species, and to make available a large number of scattered records on the occurrence and habits of this fish.

Long thought to be identical with the Pacific form, the systematic relationships of *L. surinamensis* have been treated in various papers by Gill (1882), Jordan & Thompson (1911), and Fowler (1931). This latter author still synonymizes the Pacific form with *surinamensis*, although there seems no reason to doubt that *Lobotes pacificus* Gilbert, as differentiated by Meek and Hildebrand (1925), is a valid species.

Known variously by the vernacular names of "grouper," "black grouper," "black drum," in the territory about the Indian River of Florida, the triple tail is also called the "black snapper" about Tampa, and by the names "whiting" and "sea sand fish" in Jamaica (Jordan & Rutter, 1897).

The range of this species is extremely wide, and it has been recorded from most of the tropical and semitropical waters of the Atlantic. It is found in the West Indies about Cuba (Poey, 1881), Jamaica, San Domingo (Cuvier & Valenciennes, 1830), Haiti (Beebe & Tee Van, 1928), and Porto Rico (Evermann & Marsh, 1900), and off the coasts of Panama (Meek & Hildebrand, 1925), Surinam (Block, 1785), Brazil (Ribiero, 1918 & Von Ihering, 1897), and Uruguay (Berg, 1895) in South America. Eastward it has been recorded from Italy in the Mediterranean (Doderlein, 1875).

Data on a number of specimens from off West Africa are also available. Peters (1877) examined specimens from Mungo, Victoria, and the Cameroons. Pellegrin (1913, 1914) records the fish from Dahomey, and Osorio (1890, 1898) lists it from Sao Thome and Principe Islands.

In American waters the territory inhabited by *Lobotes* extends along most of the Atlantic and Gulf coasts.

One of the earliest and certainly one of the most northerly records is that given for Massachusetts by Baird (1873), who recorded it from Wood's Hole, as did Smith (1898). The latter author also mentions a specimen from Menemsha Bight, remarking that the species was rare in those waters. Baird's specimens were caught in August, 1873; that from Menemsha in the same month in 1890, and other specimens in the National Museum are labeled December, 1875, and September 20, 1886.

Rhode Island records are not so numerous, although Kendall (1908) lists it from Narragansett Bay, remarking that in 1899 it was accounted a common fish by Rhode Island Fishermen at Pine Hill. Tracy (1906) saw this fish at Saunderstown, and Sherwood and Edwards (1901) encountered it at Prudence Island, where a specimen 22 inches in length and weighing 6 pounds was caught in a trap on September 10. Nevertheless, they considered it a very rare visitor in those waters "not more than six specimens having been recorded from this vicinity in the last twenty years."

New York occurrences are somewhat more plentiful. Mitchill (1815), under the name of *Bodianu striourus*, gives the earliest (?) American notice of *Lobotes*. DeKay (1842) says that this species, which "is sometimes called 'Black Grunts,'" is "rare in our waters," which "forms the limit of its most northerly range."

New Jersey is on a par with New York, and for this state the earliest record is again that of Mitchill (*loc. cit.*) who obtained a 13½" specimen on the New Jersey shore at Prowle's Hook. Abbott (1869) mentions the species, but Goode (1903) is incorrect in his statement that Baird (1855) took several specimens about 3" long from the eel grass of the Tuckahoe River. Baird's *Lobotes emarginatus* was shown by Bean (1887) to have been the young of *Lutianus griseus* (Linn). Fowler (1922) saw an adult taken from New Jersey waters on June 8. The specimen weighed about eight pounds. Papers by Nichols (1914) and by Breder (1925a, 1926, 1929) are concerned principally with the presence of *Lobotes* in Sandy Hook Bay, but these authors (1934) also state that it is of intermittent occurrence in New York and southern New England.

For Delaware no data have been discovered, although the fish undoubtedly occurs off those coasts. Uhler and Lugger (1876) furnish the single record for Maryland, stating that the triple tail is "occasionally caught in the lower part of Chesapeake Bay." From Virginia there are more numerous occurrences. Fowler (1912) observed this species in the market at Norfolk. Hildebrand and Schroeder (1927) record it from Lynnhaven Roads, Cape Charles, Buckroe Beach, and Ocean View, Virginia, and state that virtually the entire catch, which in 1922 was estimated not to exceed 1000 pounds, was sold in the market at Norfolk.

Kelley's paper, giving the abundance of this fish in North Carolina, has already been noted, and no new data are available from either that state or South Carolina. From this latter state we have the records of Holbrook (1855), who says that the fish is found there from June to September, and of Smith (1893). In addition, Gudger (1931) records the fish from St. Helena and Port Royal Sounds.

Georgia presents several records, according to Gudger (*op. cit.*), who reports them from Calibogue Sound at the mouth of the Savannah River, from the mouth of the Altamaha, and from St. Andrew's Sound, "the conjoined mouths of the Saltillo and Columbia Rivers."

There are additional records for Florida that should be added to those

given by Gudger (1931), by Hughes (1937), and by Baughman (1941). Evermann and Bean (1896), speaking of the occurrence of this species in the Indian River, say that it is most plentiful in the southern portion of that stream. "None were observed north of Fort Pierce, but from that place southward a few were found at each fish house It is said to come into the river in December, and go out in the spring." Wilcox (1896) also lists it from this locality, while Goode (1879) notes its presence in the St. John's River at Arlington. An additional record has been furnished me by Dr. Carl L. Hubbs. He writes that while seining in the surf on August 17, 1936, just north of Hollywood, in Broward County, Florida, he netted a triple tail 49 mm. standard length. A record by Henshall (1894) was overlooked in my 1941 note, as was another by Jordan and Swain (1884) from Pensacola.

No further data have been noted from Alabama and Mississippi, but in Louisiana, at Cameron, one immature specimen was taken by Weymouth (1911).

Texas occurrences have already been reported,* but recently a record of *Lobotes* presence at Boca San Antonio, an entrance to the Laguna Madre, in Tamaulipas, Mexico, was sent me by one of a party of fishermen who made the trip to that place.

This widespread distribution, greater than that of any other non-pelagic species, may be accounted for by the habit of the young, which often float great distances in the Sargassum weed, a circumstance that was noted by Tee Van (1930).

A number of parasites have been recorded for *Lobotes surinamensis*. The acanthocephalid *Echinochinchus pristis* Rudolphi was recorded by Linton (1891) as present in the intestine of a specimen. The cestode *Synbothrium filicollis* Linton (1897a) occurs in the viscera and the trematode *Gasterostomium ovatum* Linton (1897) has been found in the intestinal tract. Two nematodes, a species of *Ascaris*, which inhabits the intestine, and *Ichthyonema globiceps* Rudolphi are also listed by this author (1899a, 1899b) as appearing in Wood's Hole specimens, and, in his original paper (1898) on *Ichthyonema*, he notes that the infestation was very heavy, both in the peritoneum and viscera of his specimens. Bassett-Smith (1899) found the form, *Lobotes erate*, from Java, to be a host for the copepod *Caligus tenax*.

Breder (1925b) noted the feeding behavior of *Lobotes* in the following words:

In many forms with large terminal, or nearly terminal, mouths, but with comparatively short snouts, the method of taking food is peculiarly simple. When the fish's mouth is close to the desired object, it is suddenly opened widely, thus causing a current to rush inward and fill the increased oral cavity. The food is carried in on this current, and is prevented from emerging again both by the descending teeth and the fact that the current continues in its backward trend, for most of the water passes out through the gill clefts, as in ordinary respiration. Large *Promicrops itaiara* and *Lobotes surinamensis* show this particularly well.

* Since the above was written, Woods, Loren P., Rare Fishes from the Coast of Texas, Copeia, 1942(3):191-192, has noted 3 more specimens from the region about Corpus Christi.

Data on the eggs and larval stages of the triple tail have been given by Ranzi (1931), who obtained his specimens in Mediterranean waters.

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Cranial Characters of a Dog-Coyote Hybrid

E. Raymond Hall

In April, 1941, as my wife and I were driving eastward through the Black Hills of South Dakota, we visited the zoo in Custer State Park and examined the caged animals there. One canid was of a kind unknown to me; as it stood far back in its cage facing us a red ruff of hair on its chest and lower neck was prominent. A ten year old boy who chanced by on his bicycle informed me that this creature was a cross between a caged female coyote and the boy's wire-haired fox terrier. Written request for the skull of the hybrid when it died resulted in receipt of the skull on January 21, 1942. In a letter dated February 16, 1942, E. L. Burns wrote that the hybrid was approximately 10 months old when it died and the offspring of a female coyote 3 years old and a wire-haired fox terrier 5 years old.

Comparisons of cranial features of the hybrid (Mus. Vert. Zool., catalogue no. 97831, sex ?) with a coyote (*Canis latrans nebracensis*, Cherry County, Nebraska, Mus. Vert. Zool., no. 61409, sex ?) of about the same age and with a wire-haired fox terrier (*Canis familiaris*, ♂, Mus. Vert. Zool., no. 98106) weighing 22 pounds and four years old (older than either the hybrid or coyote) reveal noteworthy differences (see Figs 1 and 2).

Ten selected morphological differences judged, after examination of additional skulls of dogs and coyotes, to be of racial (as opposed to merely individual, secondary sexual, or ontogenetic) significance are as follows:

CHARACTER	COYOTE	HYBRID	DOG
frontal sinus	uninflated	intermediate	inflated
orbital angle *	41	48	58
rostrum	narrow	broad	broad
angle in maxillo-jugal suture	acute	intermediate	obtuse
general size	large	large	small
tympenic bullae	inflated	inflated	uninflated
teeth, size and spacing	large, close set	large, close set	small, spaced
taloid of M ₁	long	long	short
position of deuterocone** of P ₄	anterior	posterior	posterior
inner half of M ₁	large	large	small

* As defined by Ilgin (Journ. Genetics, vol. 42, p. 387, fig. 2, 1941).

** Inner cusp.

The resemblances to the coyote are about twice as pronounced as to the dog. Memory indicates the same to have been true of the external features, namely, color, size and build.

These are all of the available facts. It seems useless here, now, to suggest factors for the characters. The person who does can profitably consult the

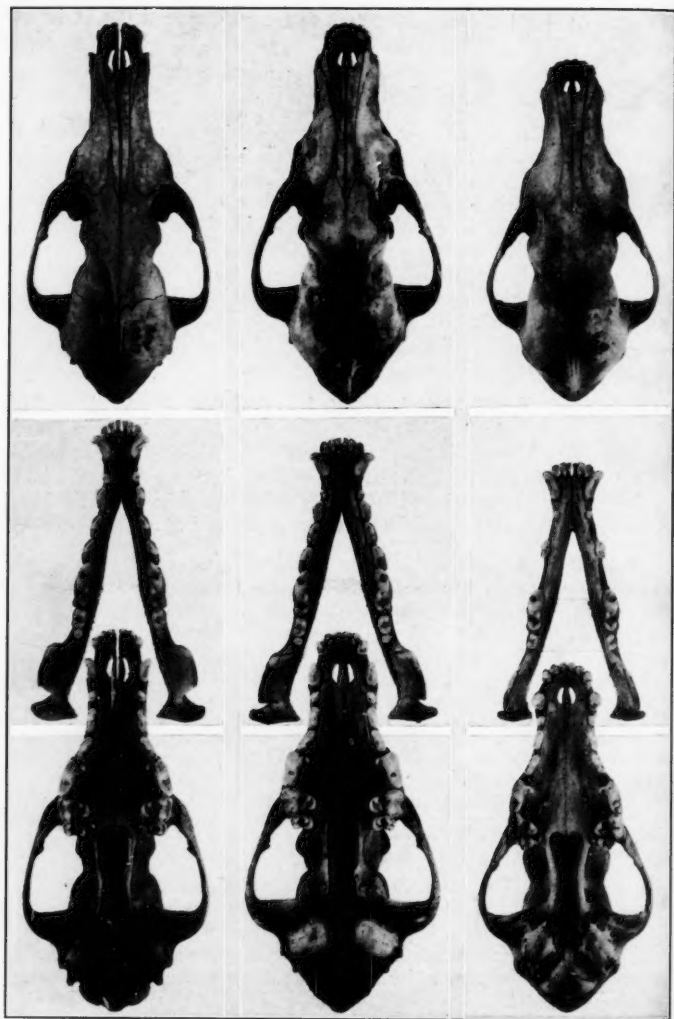


Fig. 1. Canid skulls, all $\times 1/3$. Coyote on left; dog on right; hybrid in center. Photos by W. C. Matthews.

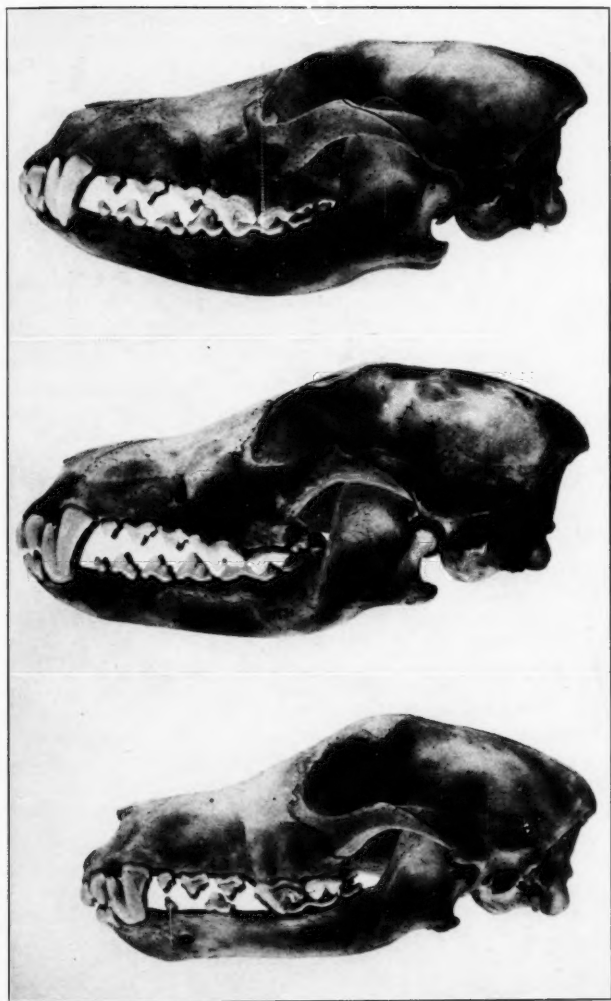


Fig. 2. Canid skulls, all $\times 1/2$. Coyote at top; dog at bottom; hybrid in center. Photos by W. C. Matthews.

paper "Wolf-dog genetics" (Journal of Genetics, vol. 42, no. 3, pp. 359-414, illustrated, July, 1941) by N. A. Ilgin. Three successful matings of coyote and dog are all that I know about. One of these was between a Siberian type of male dog from Saint Lawrence Island and a female coyote from Colorado (O. J. Murie, Dog skulls from St. Lawrence Island, Alaska, vol. 2 of the Miscellaneous Publications of the University of Alaska, p. 355, 1936). Through injury which resulted in the death of the pregnant coyote, the three young *in utero* died after a gestation period of about 65 days. The other instance is that recently recorded by L. R. Dice (A family of dog-coyote hybrids, Journ. Mammalogy, vol. 23, p. 187, 1942) in which three young resulted from a cross of a male hound and a female coyote. Dice (*loc. cit.*) had evidence suggesting that his hybrids were sterile. At the time of death the oldest of these pups was 8 months. Remembering that the hybrid from South Dakota was said to be about 10 months old when it died, a person may wonder if dog-coyote hybrids ever live to be as much as one year old. Also, all so far reported are the result of crossing between male dogs and female coyotes.

Of the three wild species of *Canis* in North America, numerous fertile hybrids have been produced by crosses between wolves (*Canis lupus*) and dogs. At least 3 crosses have been reported, as mentioned above, between the coyote (*Canis latrans*) and dog but none so far as I know has been produced by mating between the dog and the red wolf (*Canis niger*). In morphological characters and in geographic range the red wolf is intermediate between the wolf and the coyote.

In review: A third instance of crossing between a coyote and a dog is recorded; the cranial features of an undoubted hybrid are described; and attention is called to the absence of any recorded instance of crossing between the red wolf and the dog.

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Intergradation Versus Hybridization in Ground Squirrels of the Western United States

E. Raymond Hall

By modern students of living mammals the test almost universally accepted for subspecies and species is intergradation (crossbreeding) in nature, or lack of it, respectively. If crossbreeding occurs freely in nature where the geographic ranges of two kinds of mammals meet, the two kinds are treated as subspecies of one species. If at this and all other places where the ranges of the two kinds meet or overlap, no crossbreeding occurs, either directly or through connecting kinds, then the two are regarded as two, distinct, full species.

Although this concept is useful as far as it goes, every mammalogist who works with subspecies and other systematic categories lower than the genus knows that the concept as expressed above does not go far enough to cover all situations found in nature. The beginning investigator, for example, having found a mammal with intermediate characters may well ask, first if it is an intergrade or instead a hybrid and second, what is the real difference between the two? The invariable answer that hybrids are crosses between species and intergrades are crosses between subspecies is of course of no help to the beginner, but he sees more of the picture when it is explained that hybrids are often produced by animals in captivity and rarely by animals in nature, and that if in nature in the one area where the geographic ranges of two kinds of mammals overlap, only 3, let us say, of the 100 offspring produced are of mixed ancestry, these "crosses" are properly to be spoken of as hybrids whereas if, say, 85 of the 100 offspring are of mixed ancestry then the crosses are properly to be spoken of as intergrades. Where the line, in between 3 per cent and 85 per cent, is to be drawn would in some degree depend on personal opinion. Furthermore the percentage selected by any one biologist for the dividing point probably would, and I think should, vary from one instance to another depending on the geographic ranges, nature of the habitats occupied, and some other attributes of the two kinds of mammals involved.

Usually, in my experience in 95 or more per cent of the instances, where crossing occurs in nature between two kinds of mammals it is clearly intergradation. The exceptions are emphasized because in the first place their rarity excites interest. In the second place, and more importantly for an understanding of the *modus operandi* of species-formation in nature, an exception once recognized, may reveal if carefully studied, in the field as well as oftentimes profitably in the animal house, one of the previously unreported stages passed through by animals in the process of nature's formation of two species from one. Not long since, I called attention to a seeming exception to the usual case of crossing (Revision of the rodent genus *Microdipodops*, zool. ser., Field Mus. Nat. Hist., vol. 27, pp. 233-275, 1941) and offered an hypothesis (*op.*

cit., pp. 236-239) to account for the existence of 3 mammalian individuals which I regarded as hybrids produced in nature. Those three individuals, and one *Citellus*, and possibly all 3 *Citellus* listed below, are all that I have found in examining wild-taken mammals—6 in all. I calculate that in all I have studied 100,000 specimens of American mammals closely enough to recognize hybrids if there were any. My guess is, therefore, that among wild mammals of North America, hybrids do not occur more often than once in every 15,000 individuals. Of course the mere number of specimens examined in this regard is not particularly important; more important is the number of specimens studied from areas in which two species potentially capable of crossing occur together. This and many other sources of error enter into my figure of 1 in 15,000 and justify designation of it as a guess.

With this background, the situation as regards three currently recognized

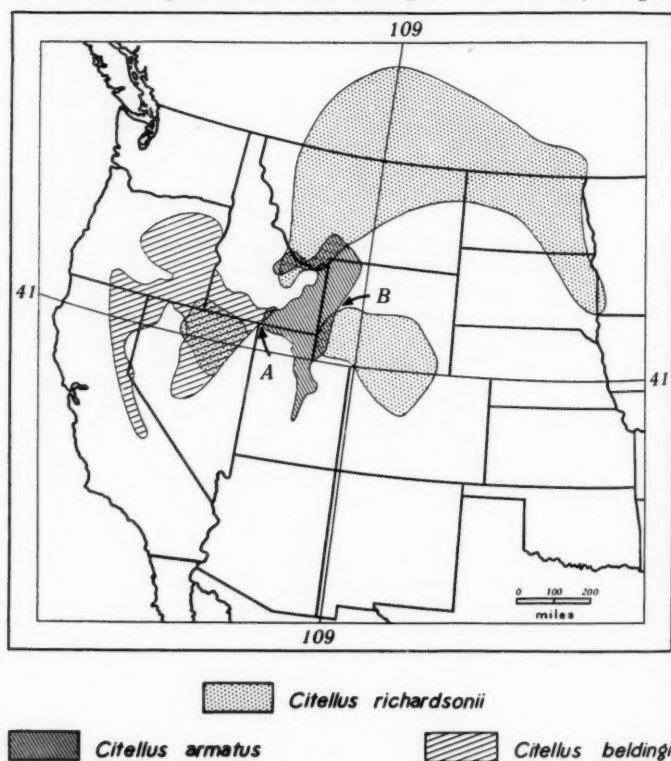


Fig. 1. Map showing geographic distribution of three kinds of ground squirrels, each currently recognized as a distinct full species.

species of ground squirrels may be stated as follows. The three species of ground squirrels *Citellus richardsonii*, *Citellus armatus*, and *Citellus beldingi* (see Fig. 1) are placed by all students of the group in a single subgenus, and are regarded as closely related even within the subgenus, but are regarded as comprising three distinct species. The first species, *richardsonii*, has been divided into 4 subspecies (see A. H. Howell, Revision of the North American Ground Squirrels . . ., N. Amer. Fauna, no. 56, 1938; W. B. Davis, The Recent Mammals of Idaho, Caxton Printers, Caldwell, Idaho, 1939); the second, *armatus*, has not been subdivided (Howell, *op. cit.*, p. 79); the third, *beldingi* has been divided into 3 subspecies (Howell, *op. cit.*, pp. 81, 85; E. R. Hall, A New Race of Belding Ground Squirrel, Murrelet, vol. 21, pp. 59-61, 1940).

Between subspecies within these species I have noted scores of individuals which properly are termed intergrades according to the test outlined above in the initial paragraph.

Davis (*op. cit.*, p. 169, fig. 8) was the first to find that the geographic ranges of *armatus* and *beldingi* met. This was in southern Idaho at the place marked A on Fig. 1. Of the situation there Davis (*loc. cit.*) writes that the range of *beldingi* from Albion east to the Raft River

Interdigitates with that of *armatus*; often individuals of both species occur in the same general area. . . . each colony usually consists of individuals of but a single species and there appears to be but little intermingling of the two. That cross-breeding does occur is evidenced by a single male specimen (no. 67468, Mus. Vert. Zool.) from the Wickel Ranch at Elba where both species occur in the meadow along Cassia Creek. This individual resembles *oregonus* [= a subspecies of *Citellus beldingi*] in having the lower surface of the tail reddish, and the individual hairs of the tail banded with red, black and white. In general dorsal coloration and in most of the cranial characters it is like *armatus*. Hybridization appears to be infrequent because evidence of it was found in only one of thirty-nine specimens of both species collected from the area where the two are known to occur together. I was unable to detect any differences between the two in habits or habitat preference and, where they occur together, I infer that they compete.

At another place, B on Fig. 1, 2 specimens, conventional study skins accompanied by cleaned skulls and the usual data including external measurements, were taken on August 23, 1939, by Donald T. Tappe, 15 miles northwest of Pinedale, 7600 feet elevation, Sublette County, Wyoming. No other ground squirrels were saved from here. Each of the two appears to be of mixed ancestry as between *Citellus armatus* on the one hand and *Citellus richardsonii elegans* on the other hand. Comparing specimens of the two kinds from other localities in western Wyoming, outstanding differences are in *armatus*: upper parts darker; tail grayish, not buffy beneath; ear longer as measured from the notch to tip.

Specimen no. 88988, taken by Tappe, is almost exactly intermediate in color of upper parts; nearer *richardsonii* by a decided degree in color of lower surface of tail and like *armatus* in length of ear. The second specimen, no. 88989, taken by Tappe, is colored on the upper parts almost, if not exactly, like *armatus*; has decided evidences of the buff characteristic of *richardsonii* on the underside of the tail but even so is in this respect nearer *armatus*; has an ear short, about as in *richardsonii*.

Howell (*op. cit.*, p. 80) comments on the fact that at Pinedale and Cokeville, western Wyoming, the two kinds of squirrels "occupy the same ground." He gives not the slightest hint that crossing occurs. Indeed he practically states the opposite when he writes (*loc. cit.*) that "The Uinta ground squirrel [= *armatus*] is a distinct species. . . . The range of *armatus* meets and slightly overlaps that of *elegans* in parts of Montana and Wyoming, but in general this species occurs at higher altitudes and in more heavily wooded areas than does *elegans*."

Of the three ground squirrels mentioned by catalogue number, that from Idaho appears to be a hybrid. The two from Wyoming may be hybrids or may be intergrades. Field studies and collecting of specimens will be required to tell which they are. If intergrades, the classification of these squirrels will have to be changed (*armatus* becoming a subspecies of *Citellus richardsonii*) and the situation will be an especially interesting one to study because the two kinds of ground squirrels probably are connected at only this one of the places where their ranges meet. This poses the further question: Is this a case in which we can observe the final stage in the separation of one species to form two full species or instead is this a case in which two species have long been separated and now crossbreed at only one or a few of the places where they occur together after changes in geographic range brought them together again.

If the animals from Wyoming by further field study prove to be hybrids, the same question presents itself. The field work necessary for solution of the problem is slight.

It may be added that although specimens are available from the two other areas where two of these species occur together, they show no evidences of crossbreeding. Perhaps this is because no effort was made in the field work to obtain evidence on this score. The two other areas referred to are (see Fig. 1) northern Nevada where *Citellus richardsonii nevadensis* and *Citellus beldingi crebrus* occur together, and along the southeastern part of the boundary between Montana and Idaho where *Citellus richardsonii aureus* and *Citellus armatus* occur together.

The tenuous connections between nascent species and the fragile reconnection between full species as revealed in the past few years by systematic studies of the Mammalia—the class of organisms to which man himself belongs—in western North America, tremendously increases the opportunity, through wisely planned field studies, for understanding fundamental and critical steps in the formation in nature of species. Because the ground squirrels do well in captivity, the scope of the opportunity is wide enough to give room for the purely laboratory student of genetics. To focus attention on this opportunity, probably illustrative of others along the eastern face of the Rockies, is the main purpose of this note.

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May Food Habits of Armadillos in Eastern Texas

Rollin H. Baker

In connection with other field investigations a collection of stomachs of the armadillo (*Dasypus novemcinctus texanus*) was made during May, 1942, in Polk and Trinity counties, Texas. The food habits material was obtained during the nesting season of bobwhite quail (*Colinus virginianus*), and it was hoped that a sufficient number of stomachs could be collected to merit some conclusions concerning the question of the armadillo predation on quail eggs, which is a popular acknowledged fact among the residents of eastern Texas. However, only 25 stomachs were taken, too few to offer any solution to this question but because little has been recorded regarding the food habits of the armadillo, the results of the examination of the material appear worthy of being listed. The stomach contents were examined by the author.

The animals were shot in open pine woodland during late afternoon, a time when armadillos are actively engaged in feeding. As a result most of the stomachs were quite full, containing, on the average, 64.2 cc. of material. Insects constituted the bulk of the food items, being 77.4 percent of the total volume of the 25 stomachs. Angeworms occupied 13.57 percent of the bulk while other animal food, including 3 vertebrate items, consisted of only a small percentage. Interesting is the fact that 2.6 percent of the stomach contents was blackberries. Grass and small roots were present as traces in 12 stomachs. Sand and mud were found in all stomachs, constituting 4.37 percent of the bulk. Table 1 lists the food items in the 25 armadillo stomachs. Table 2 presents a list of insect food items.

TABLE 1.—List of Food Items Found in 25 Armadillo Stomachs

Food Items	Percent of Volume	Frequency	Volume in cc.
Hexapoda (Insects)	77.40	25	1241.9
Annelida (Angeworms)	13.57	24	217.7
Debris (Sand and Mud)	4.37	25	70.2
Blackberry	2.60	2	41.7
Chilopoda (Centipedes)77	23	12.5
Reptilia (Unidentified Lizards)65	2	10.0
Diplopoda (Millipedes)25	12	4.0
Amphibia (Unidentified Salamander)21	1	3.4
Mollusca (Slug)18	1	3.0
Crustacea (Sow-bug)	TRACE	1	TRACE
Crustacea (Crayfish)	TRACE	2	TRACE
Arachnida (Spider)	TRACE	1	TRACE
Arachnida (Scorpion)	TRACE	1	TRACE
Roots and Grass	TRACE	12	TRACE
	100.0 percent		1604.4 cc.

TABLE 2.—List of Insect Food Items in 25 Armadillo Stomachs

Food Items	Frequency
Scarabaeidae (Adults and Larvae)	23
Carabidae (Adults)	20
Elateridae (Larvae)	20
Lepidoptera (Larvae and Pupae)	13
Orthoptera (Adults and Eggs)	13
Formicidae (Adults and Eggs)	10
Lampyridae (Larvae)	6
Chrysomelidae (Adults)	2
Isoptera (Adults)	1
Diptera (Adults)	1

The results of the examination of the small amount of material appear to show that armadillos feed generally on insects though readily eating any other animal life uncovered in their probings, the former being most commonly encountered. No quail egg remains were discovered, but it is not unlikely that such items are eaten by armadillos. Though these animals are quite abundant in the best quail habitat of eastern Texas, it is probable that the chances of the armadillo finding nests during its quest for food are not as great as made out by local quail hunters. Roots and grasses are utilized, though perhaps accidentally in some cases. Blackberries were found in 2 stomachs.

If these food items are near typical, this study indicates that armadillos are rather beneficial, feeding on destructive insects, their pupae, larvae and eggs, though in their quest for these foods, certain beneficial forms are also taken including the carnivorous beetles, centipedes, angleworms and others.

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The Origin of Wings and Venational Types in Insects

William T. M. Forbes

There have been many theories as to how the wings of insects arose, and from what parts of the body they were derived, but with increase of knowledge of the morphology most of them are either wholly abandoned or considered very improbable. Most insect morphologists now agree that the wings are in some way derived by the extension of the lateral edges of the dorsal sclerites of the two segments (mesothorax and metathorax) to which they are attached, and that they served to plane through the air, more or less like a flying squirrel or a flying fish, before true flight was developed.

In a similar way the theories as to the pattern of wing veins have evolved with increasing knowledge of the details, until we now have agreement that there is a fundamental pattern from which all the insect venations are derived, though there is still a good deal of argument as to the equivalence of particular veins in the different orders. The remaining points of argument have come to be mainly the following: 1, whether the dragon flies and may-flies can be properly compared to each other, and, whether or not, the relation of their veins to those of other winged insects; 2, whether the difference between convex and concave veins is more or less significant than the patterns of the pupal and nymphal tracheae, and if important, which veins were originally concave; 3, whether the front branch of the vein called media is homologous in all orders of insects, and if not, whether the vein called R_{4+5} in some orders is the equivalent of the one called "media anterior" in others by some authors; 4, whether the "axillary" or "anal" veins can be directly compared in the different groups of orders, or whether they must be considered to be several different selections from an originally amorphous series; and 5, to what extent the veins in the various fossil insects loosely grouped as "Palaeodictyoptera" can be homologized to those of living insects.

The following account is planned to give a key to the present state of our knowledge, and attempts an answer to these questions. I have assumed that the illustrations in three standard works are at hand: Comstock's "Wings of Insects," Snodgrass's "Principles of Insect Morphology," and Handlirsch's "Die Fossilen Insekten," but believe that the figures included in this paper are enough to explain the general line of the argument.

The Origin of Wings

We must start with the condition of the two posterior segments of the insect thorax as it was shortly before the beginning of wings. Figure 1 is so drawn as to be comparable with Snodgrass's figure 91, p. 165, in the "Principles of Insect Morphology." The *tergum* (T) formed a broad plate, the whole width of the body, ending in a flange, *W*, along each side (shaded in the

figure), whose lower as well as upper face belongs to the tergum. On the side of the body below this lies the *pleura*, bisected by a vertical infolding, the *pleural suture* (*Pls*) dividing it into the anterior *episternum* (*Eps*) and posterior *epimeron* (*Epm*). Internally this infolding was a heavy flange (Snodgrass Fig. 92), ending in a knob above, the *wing process* (Fig. 1, *W. P.*), which supports the lateral flange of the tergum at a single point near its middle, that we shall call the *fulcrum* (its position marked by an asterisk*, in Figs. 2 and 3). The tergum was also subdivided, but only the *scutum* (*Sct*) and *scutellum* (*Scl*) have relation to the developing wing, for the lateral flange is an extension of them only, and the postscutellum and phragmas are excluded. The musculature of body wall and legs was, of course, already highly developed, but we must call special attention to two leg-muscles running from the upper edge of the pleura to the coxa, a *basalar* (*3E'* of Snodgrass's Figs. 102C, 103, etc.) and a *subalar* (*3E''*), respectively muscles E and F of Snodgrass's "Morphology and Mechanism of the Insect Thorax," *Smiths. Misc. Coll.* vol. 80, no. 1, 1927.

A third preëxisting structure that is drawn into the formation of the wing is the tracheal system. A characteristic of the insect tracheation except in a few of the lowest Apterygota is that longitudinal trunks are formed on each side by the anastomosis of a branch of the leg trachea of each segment with the anterior trachea of the following; this compound trachea becomes very large, and in the abdomen of the caterpillar runs in a distinctive way ectal to the deepest fibre or two of the transverse lateral muscles. In the thorax the large longitudinal trachea that takes its place runs ental to the *entire* musculature, even the fibre which corresponds to the innermost one on the abdomen, but comparative study shows that there is another more ectal trachea, in the position of the abdominal one, and this trachea is produced in some forms by the anastomosis of a leg trachea in front with a primary trachea of the segment behind.¹ This one is the tracheal loop which supplies the wings, and is shown in diagrammatic condition by the very primitive Neuropteran, *Chauliodes* (Chapman in Comstock's "Wings of Insects" p. 32, fig. 20). I would suggest that this one was originally the continuation of the longitudinal trunk of the

¹ Šulc in *Acta Soc. Sci. Nat. Moraviae* iv, pp. 283, etc., 1927 (*Zool. Rec.* 1930), would equate the two main tracheal stems of the wing to the two main tracheae of the paranotal lobes of *Machilis*. Unfortunately for his theory the basal connections are entirely different. In the winged insects the anterior stem comes from the leg trachea of the same segment, the posterior from the anterior side of the spiracular tuft of the following segment. But in *Machilis* as figured by Šulc the first comes from the dorsal and the second from the leg trachea of the same segment. I incline to the theory that the wing-tracheae have developed from the longitudinal trunk after it was formed, and that it is not homologous with the more dorsal series of anastomoses in *Machilis*, though the latter may become the *definitive* longitudinal trunk of the thorax, as it obviously is in the cockroach (Comstock, *Wings of Insects* 31, fig. 18). It would still be possible to save Šulc's plan by modification—assume that the anterior trunk of *Machilis* was wholly lost, that the posterior trunk, which *does* come from the leg trachea, and does supply most of the paranotal lobe, becomes the anterior one of winged insects, and that the posterior trunk is secondary. In fact this is minute and almost always overlooked in the may-flies, and was omitted by Šulc in his may-fly figures.

abdomen, and that its smallness and late appearance was a secondary effect of its having become involved in the wing, — so sharing its late development.

The nerves to the sensory organs of the wings are probably of at least equal importance, and in the finished wing accompany the tracheae within the veins,² but we know too little about their history and basal connections to bring them into our history. This nerve is morphologically the anterior lateral one, and supplies most of the segmental muscles as well as the wing.

Before the commencement of wings, then, we have on each thoracic segment a chitinized shelf-like extension of the tergum, supported a little behind the middle by the pleural ridge, and with an important longitudinal trachea running along it within, and supplying it with tracheal twigs. The shape of the flange would doubtless cause these twigs to take the form of a single longitudinal series.

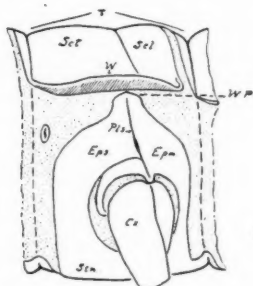


Fig. 1. Hypothetical Segment of Thorax, before Wings; side view.

First Stage of Development

Present theories of the first rudimentary approach to flight may be divided into two groups. According to one school the pre-flying condition took the form of a strongly flattened insect, essentially like an apterous cockroach or *Machilis*, that developed the habits of climbing up the trunks of the Devonian trees and planing off to a new locality, as many of the apterous cockroaches are still in the habit of doing. Others would have in mind an insect that was at home in the water, and developed the habit of leaping out from time to time like a flying fish. One may call these two the flying squirrel and the flying-fish schools. What follows is developed on the squirrel theory, but its application to the flying-fish theory would call for merely minor changes.

We have then a flat insect, — a pre-cockroach, — with the habit of leaping and planing like a flying squirrel. In such a creature any increase of width of the lateral flanges would make for longer flight, and a special widening rather

² See e.g. Racięcka, O unerwieniu skrzydeł u Rhopalocera. Prace Zakładu Zoologicznego Uniwersytetu St. Batoregu w Wilnie, vol. iv, no. 12.

in front of the center of gravity would be very useful for control. So I postulate an insect in which a couple of segments (the meso- and metathorax) are specially extended in the form of lobes such as are shown in top view in Fig. 2. In this figure I have shown the longitudinal trachea (the ancient one, not the one of modern larvae) with the portion marking the link between its two original trunks dotted. I have shown the tracheal twigs which support the flange, now at least arranged in a single series, and with the usual tendency of tracheae to dichotomize. I have figured the one in the middle of the series, where the flange has become widest, as already having a double dichotomy, but this may perhaps be an anticipation of a later condition. An important feature of this stage, however, is that the foremost twig supplied by the trunk from

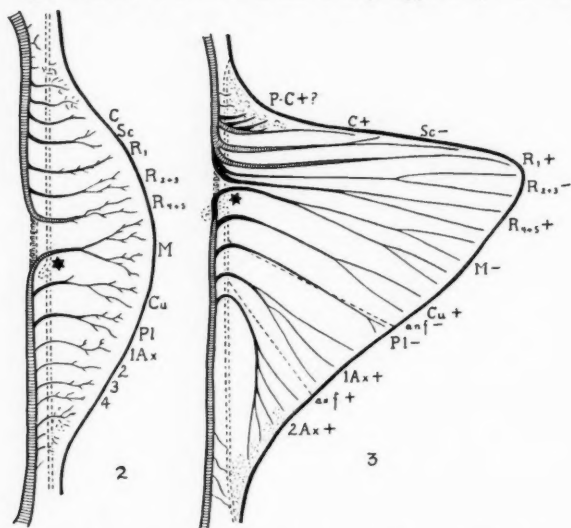


Fig. 2. Hypothetical planing wing with tracheae; early stage. Fig. 3. Same; fully functional stage.

the spiracle behind runs around *in front* of the fulcrum (*), a fact very noticeable in later evolution, and one indicating that at this stage the pleural suture did not have its forward slant, so characteristic of all flying insects except the Odonata, but had its upper as well as its lower end well behind the middle of the segment. This is still the condition in *Thysanura* (e.g. *Japyx*, Snodgrass, Sm. Misc. Coll. lxxx (1) fig. 10.) or to a less degree even in *Heterometabolous* nymphs (l.c. fig. 13).

We can assume that muscular action will be of some slight effect even at this stage, if as is probable, the chitine was somewhat flexible. Even though the material later to become the basalar and subalar sclerites, was doubtless

still the upper edge of the pleura, contraction of the basalar muscle (3E' of Snodgrass '35, E of Snodgrass '27, p. 65, fig. 28) would obviously pull the front of the wing down as well as move the leg, and by this warping would produce a turn toward the side whose muscle should contract. A simultaneous contraction of the subalar muscle, serving to immobilize the leg, would also aid the warping of the wing, even at this stage.

Second Stage

The line of evolution would obviously go in the direction of greater support and more effective steering, since true flight would hardly yet be possible. The first need would lead to a direct increase of area, the second to the specific lengthening, concentration and strengthening of the portion of the "wing" controlled by the basalar muscle. We may assume that by this time the tracheae (and their accompanying nerves, of course) had come to a definite number in the broader portion of the flap, though still indefinite in front and behind; and we may now tag them with the familiar names (Fig. 3). I have applied the traditional names to the two figures.

This new step, as compared with figure 2, has involved the following changes: 1, the flap is longer, broadening the body for better sustentation; 2, the fulcrum has moved forward, concentrating the part of the wing controlled by the basalar muscle; 3, 4, the tracheae in the anterior portion of the wing have presumably enlarged, and this portion has doubtless come to be more chitinized (stronger and stiffer) than the posterior portion; 5, this same portion has become relatively longer, and the 4-forked M, which was the center of a symmetrical wing, has slipped back to a subordinate position in the thin part of the wing; 6, the veins which are to become Rs may well have suffered the same fate; but 7, the fulcrum and tracheal supply have kept their old relation, so that the foremost trachea supplied by the posterior trunk (M) now begins to take its characteristic wide loop around the fulcrum.

We now have a really efficient organ of gliding flight, and there is no reason why this stage might not have become a dominant and efficient insect type. If the *Psilotum* of the insect world has survived in some neglected corner of Malaysia, I should expect it to look like this.

Third Stage

The conversion of the wing just described (Fig. 3) into an actual organ of flight is a simple but distinctly odd process. All that is needed is to change the steady tonic contraction of the basalar muscle (3E') into a vibratory, clonic type. As this muscle is attached to the stiffened front portion of the wing, already developed for steering, the immediate result will be a sculling motion, and actual though weak flight. Stating it teleologically an insect that started to alight (contracting muscle 3E' to bring it down) and then countermanded the order, but so inefficiently as to throw the muscle into intermittent contraction, would automatically find itself flying. At this stage

of development we must assume that the subalar muscle ($3E''$) does not share in the clonus, but merely contracts enough to antagonize $3E'$ at the coxa and prevent the leg from moving. As long as the wing-process remained longitudinally in line with the insertions of the two muscles (as in Fig. 2) it would perhaps increase the curvature of the wing, but as soon as the wing-process had moved back into the body (as in Fig. 3) its synergistic contraction with $3E'$ would depress the wing as a whole, and it could then have served as a minor flight muscle.

At what stage of this evolution the indirect wing-muscles would begin to function as flight muscles I would hardly venture to guess. They would of course contract to fix the thorax as a concomitant to any use of other thorax muscles, but I cannot say whether they would aid the warping of the "wing" in its planing stage. The fact that they are non-functional in the Odonata

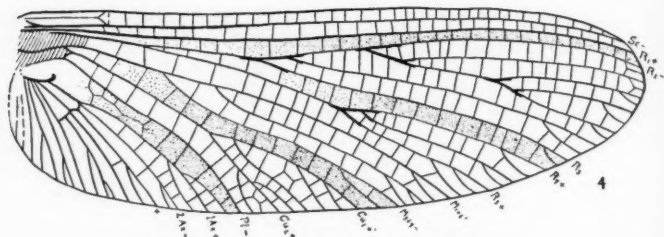


Fig. 4. Ephemera. Venation of Prottereisma.

suggests that perhaps they were only added to the flight muscles at a relatively late stage, by a secondary spreading of the vibratory impulse intended to activate $3E'$, in some form where the shape and elasticity of the thorax made such a spreading useful.

About at this point we get the modification of the wing bases which converts a series of merely bifurcated tracheae into the definitive system on which the hypothetical venation is built. An important modification of the wing as it becomes an efficient organ is the narrowing of the base, and with this the forming of a membranous hinge dorsally as well as pleurally. As a result of this the bases of the veins naturally become much crowded, and I assume that, as usual with tubular organs in such cases, there is lateral fusion of the tracheal-bases, and of the veins which come to surround them. But at this stage we get a divergence of development, which is as I believe fundamental. The veins which fuse are not the same in three main subdivisions of the winged insects: in the Odonata and Ephemera, and also in the fossil Protodonata and Ditaxineura, R_1 remains a free and practically unbranched vein; in all the residue, therein including the so-called Protephemera, — and all the varied lot now grouped as Palaeodictyoptera, — the next one or two veins have joined as posterior branches of R , and form the "sector." These latter again divide into two series, in the first, represented only by fossils, — Stenodictya and a

few related genera, — there is a single forked concave vein attached to R, and the following main stem of media starts with a strongly convex anterior branch; in the residue, including all living forms except the Ephemera and Odonata, Media is wholly a concave vein, and Radial Sector is more richly branched; I believe in the former case the second original vein behind R_1 has joined media, where it becomes the so-called media anterior (of Lameere), while in the latter it has joined radius, and become R_{4+5} . If this is correct the terms R_{4+5} and MA are mutually exclusive and should not be used in the same orders. So I should make three main venation groups: 1, R_1 free, Rs, M and Cu either free (Ephemera) or combined on a single stem (Protodonata and Odonata, including Ditaxineura); 2, R_{2+3} forming the sector of R, R_{4+5} joined to M as MA; 3, R_{2+3} and R_{4+5} both joined to R_1 , making a fundamentally 4-branched sector, and M wholly concave.

In a few primitive Neuroptera we see R_{4+5} still in a neutral state, since while it is clearly joined to R, the connection to base of M is still visible, looking like an oblique cross-veins, especially in the hind wing of Hemerobiidae and fore wing of Myrmeleonidae.³

Since all these three types have fully functional wings, we must assume that in the ancestral fully winged insect the main veins (or at least R_{2+3} and R_{4+5}) were still independent at the base.

Development of Texture

It is obvious that the first stage of the wing-flap is a mere extension of the body-cavity, containing as a matter of course all the normal components: blood-space, tracheae, and nerves leading to the tactile setae on the skin. Perhaps there may also have been portions of muscle and fat body which would later be eliminated, and it is obvious that there were structures of auditory type, for scolopae are still to be found in the large veins of most insects. The progress from this would not be the formation of veins, as usually stated, but the forming of the intervening membranes, for the veins are still extensions of the body cavity, with the essential blood-space, tracheae and nerves. There will then be two controls of the formation of the vein-patterns: 1, there must be a sufficient supply of spaces to accommodate the tracheae and nerves, to supply blood for the living tissues, and especially to expand the wing at the last moult, while between the tracheae the exoskeleton as well as the space could be thinned to save weight. The veins then were not places where the exoskeleton was thickened, but places where it was not thinned, and this probably explains the curious fact that where an injury to the nymph or pupa forms an abnormal blood-space, there is formed not a defect of the wing but a supernumerary vein (whether a trachea is present or not), while a supernumerary trachea may often fail to form a vein, if it fails to prevent the

³ *Permonera* (Carpenter, Am. Jour. Sci. (5) 22, 125, fig. 6) shows this condition strikingly. I suspect it is no longer a true Anisaxian, like *Dunbaria*, but already belongs to the Neuroptera, where it combines features of both Megaloptera and Planipennia with a point unique to itself (the loss of Cu).

collapse of the original blood-space. The tracheae, being preëxistent, however will obviously be the normal reason for blood-spaces to remain and then for veins to be formed.

2. With the thinning of the intervening areas the veins obviously also become the main strength of the wings. It is plain that this need is equal but different to the other, though both require a certain minimum of space between veins, and both require a similar connection to the base. In general we may assume that the two needs are compatible, and that a vein can take a position useful for both, though in many of the higher orders the temporary need of blood for expansion of the wings is supplied by un-chitinized veins that collapse and disappear as the wing dries, — striking cases being the fugitive net-veining of the cicadas (Am. Nat. 56, 191, 1922) and 1st A and the base of M in all but the lowest Lepidoptera. The reverse condition obviously cannot exist, since blood will be necessary in any case for the secretion of the hard skeleton (sclerotization) *after* expansion is completed.

It is an interesting question whether the cockroaches may not owe the thickness of their elytra to the incompletion of this process; for they are the only living order whose continuous history goes back to the beginning of our record. In them the distinction between vein and cell exists, but is one of degree, not kind, the interspaces being thinner than the veins, but still supplied with a blood-space. The Coleoptera, which show the same condition even more

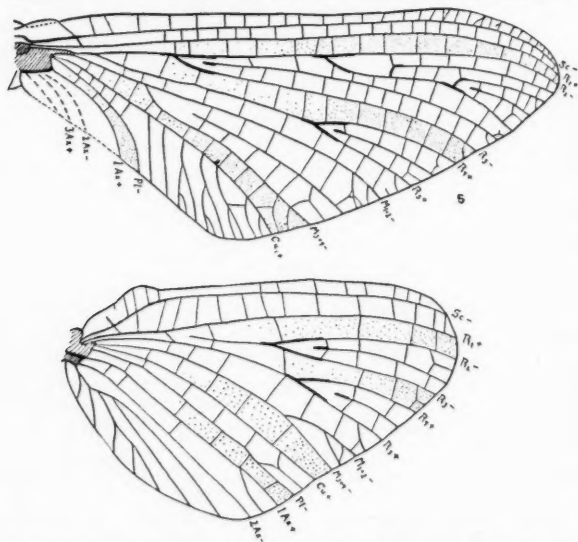


Fig. 5. Ephemerida. Venation of modern type (Siphonurus). The hind wing drawn on a larger scale.

strikingly, must be a case of degeneration, since they are obviously from the Holometabolous stem, which certainly had a long history of fully membranized wings in their ancestral Palaeodictyoptera or Anisaxia, and Megaloptera.

Development of the Hinge

We started with a long flap of elastic chitin (Fig. 2). The line of progress of such a structure as it becomes more movable is always the formation of an articulation. Obviously in the present case the need is first for a pivot, for the vertical motion which we assume in steering, and then a longitudinal hinge to serve the wing-stroke as soon as true flight is developed. The second of these needs could be served by a mere dechitinization of the line where the wing attaches to the tergum, but the first requires the shortening of the long chitinous base. We need to get a firm point of attachment at the middle of the wing, or a little in front, then a loosening of connections both in front and behind this point. The attachment is formed in fact of two structures. The *fulcrum* (*), where the wing rests on the pleural wing-process, serves to resist the down-stroke, and the media drops below the general wing-level to associate itself with the fulcrum and take the main function of support. The remaining attachment to the tergum is taken by radius, which rises and becomes the principal convex vein of the wing; it also moves back, so as to be as near as possible to media and the wing-process and form an efficient pivot. I believe it is this coming together of radius and media that crowds out sector and media anterior (or the fuller sector with R_{4+5} as well as R_{2+3} , and forces their branches to migrate onto the stem of either radius (higher insects, R_{2+3} of Stenodictya) or media (Odonata, R_{4+5} = MA of Stenodictya). Only in the Ephemera does sector keep its independence, and it does so at the cost of its base.

At about the same point of evolution we may assume the basalar and subalar sclerites became independent of the episternum and epimeron, respectively; and became small sclerites, merely serving the two direct wing-muscles. Even the Ephemera have reached this condition, though the basalar is inconspicuous and the subalar is very large and has often been mistaken by morphologists for the epimeron. In the Odonata, which are also commonly said to lack basal sclerites, the pleural ones are fully developed, but so deeply imbedded as to be easily overlooked, — they form mainly large muscle-tendons, — and are connected directly to the wing by bands of tough membrane.

We have noted that the basalar muscle ($3E'$) is now the principal if not the only flight-muscle, as well as the principal if not the only muscle for the down-warpage of the wing on landing. It makes its connection to the base of the next vein in front of R, which we can now call subcosta, and causes it to become a second concave vein. The vein in front of this again makes connection (through the tegula) with the small muscle which pulls the wing forward (one of the tergo-pleurals), and becomes the front edge of the functional wing in all forms above the Orthoptera. In these latter a few *precostal* veins may intervene, but in all other winged insects the precostals degenerate to minor twigs or disappear.

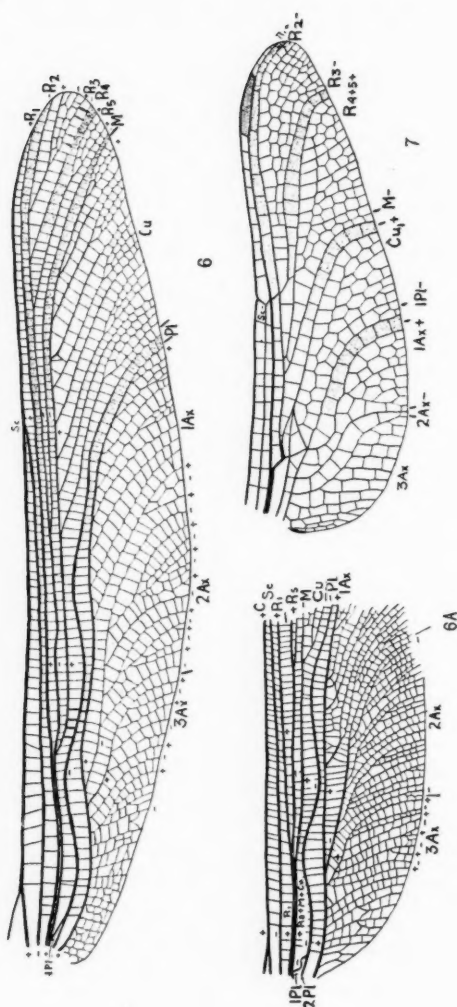


Fig. 6. Protodonata. Fore wing and base of hind wing of Typus, Fig. 7. Libelluline hind wing.

Behind the fulcrum further development takes quite different directions in the various main lines. We must first divide the flying insects into those which can fold the wings back over the body (Neoptera) and those that can only lift them up above the back, or occasionally not even that (Palaeoptera, including of living forms only the Ephemera and Odonata). In the latter there is only one step of progress in the machinery; the bases of the veins (cubital and anal-axillary group) become concentrated close behind the fulcrum

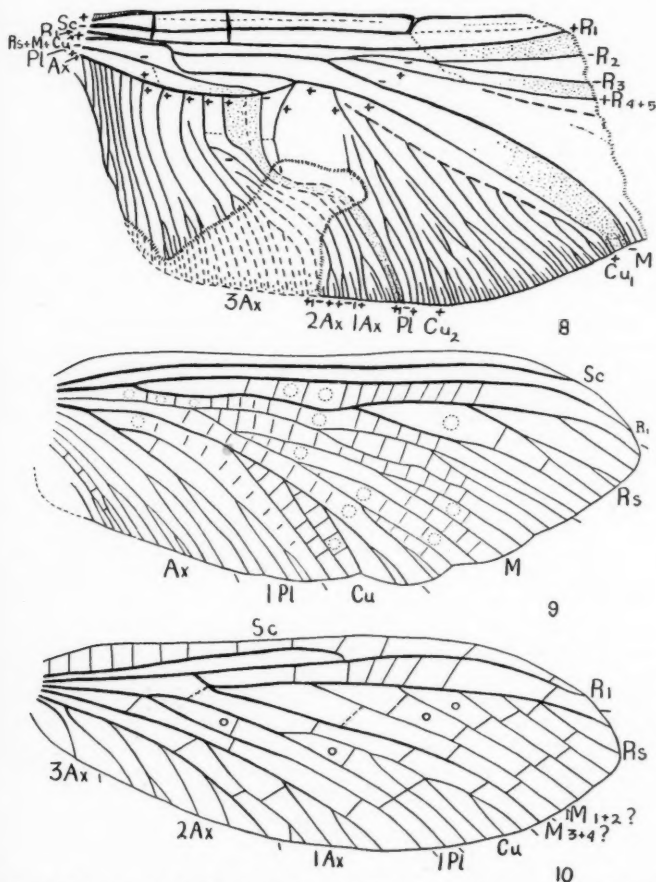


Fig. 8. Odonata. *Aeshnidiopsis flindersensis* (Wood). Hind wing. Fig. 9. Anisaxia. Lamproptilia. Fig. 10. Neuroptera Megaloptera. Diaphanoptera.

to aid the pivot-motion of the wing (rotating on a transverse axis), and at the same time are cut off from the body by a band or area of membrane which serves as the hinge for motion on the longitudinal axis. In some forms they remain numerous, though the most posterior always fuse together to a certain extent, and the second (plical, in some orders commonly called first anal, in others treated as a branch of Cu) often fuses at the base with the first (true cubitus). At this same time the extreme bases of the veins are modified into a series of thickened knobs, the *axillary sclerites*. In the Odonata and doubtless the Protodonata these remain continuous with the veins, and in the Ephemera are somewhat amorphous, but in the Neoptera the portions of the veins just beyond them become flexible, at least from front to back, and in the case of the veins behind radius often become completely membranous. In the first two cases the contraction of the axillary muscle (Snodgrass Fig. 103, D) merely pulls down the axillary sclerite to which it is attached and thereby raises the wing, in the Neoptera a further contraction pulls the sclerite in deeply, folding the wing down and back over the body, as explained more fully by Snodgrass. In the Ephemera the number of axillary veins (of somewhat uncertain homology) which reach the base of the wing or nearly so, remains large (Figs. 4 and 5); in the Protodonata and Odonata the whole axillary system fuses into a single main stem at the extreme wing-base, and its three branches a little further out may or may not represent the three axillaries of Neoptera. In the Protodonata these three main branches are clearer than in the modern Odonata (Fig. 7) and are convex, concave, convex. In the broader-winged Odonata this region is involved in a complicated system of truss-bracing, producing the *anal loop* or "boot." My own interpretation of this is based on the condition of the Protodonates, and differs from that accepted by Odonate specialists (see below) but we both agree that there is a single basal anal main stem which forks into the two or three anals further out.

The entire Neoptera, both Orthopteroids and Holometabola, agree on the pattern of axillary sclerites and the mechanism of wing folding, for the details of which see Snodgrass. Here again the axillary muscle pulls on sclerites formed by the partial fusion of the bases of the cubital and axillary veins, which are now almost independent of their outer portions. The first pull has the same effect of raising the wing, but further contraction causes it to swing back over the body, developing a convex fold through the midst of the axillary area (ax.f.+ of Fig. 3) and a second concave fold close to the body. In the hind wing of the Orthopteroids this axillary fold is close behind the Cu and Pl, only one more vein intervening (which I have called 2d Pl), but in the Holometabola the fold is frequently lower, in the middle of the anal fan. There are also frequently further lesser folds (very numerous below the ax. fold in the Blattoids other than Corydiidae s.l., Dermaptera, and Orthoptera), but these vary from order to order. In the outer part of the wing it is a question whether the so-called axillary folds are homologous (see 5th Ent. Congress, pp. 277-284) but their basal portions and functions agree absolutely. In the Holometabola, also the Psocidae and their kin, no second plical can be identified.

Another development, present at least in all the Neoptera, is a concave furrow (not a fold as often called) from base to margin of the wing just below Cu. This lies close along the (1st) plical vein, and causes it in turn to be a concave vein. It is also a line of weakness, and when it coincides exactly with the plical vein tends to obliterate it (as also does the discal "fold" when it happens to lie on a portion of media). This, as well as the discal fold when present, have no obvious function in the adult wing, and I suspect are somehow concerned in the packing of the unexpanded wing in the pupal pad. In any case they are present in all orders of Neoptera which have an ample posterior part of the wing, and in almost all members of those orders. It is my personal belief that the second or third main concave vein of the Palaeoptera can also be treated as homologous. It has the same relation to neighboring veins and to the basal articulation, and in the Protodonata is plainly supplied by a vein running sharply back from near the base of the convex vein in front of it in the same way. For this reason I interpret the so-called Cu+A of the Comstock-Needham Odonata scheme (Wings of Insects Fig. 230 etc.) as Pl. and the so-called R+M (which is really two veins closely parallel in all Odonata, Protodonata and related forms) as R_1 and $Rs+M+Cu$.

In the Ephemera the same approach will require us to choose a simple concave vein as Pl, and the obvious one is the one so labelled in Tillyard's later papers, and in Needham and Knox's "Biology of the May-Flies"; this is the vein that earlier works (e.g. Comstock in the "Wings of Insects") called 2nd A in the fore wing and Cu_2 in the hind wing. By this interpretation R_1 will be free and $Rs+M+Cu$ will form a single fan, just as in the Odonata, while in both wings the remaining axillaries will arise from a single transverse basal bar exactly as in many Orthopteroids, and the second main axillary will be a concave vein.

By this interpretation we reach a position intermediate between those persons who regard the system of convex and concave veins as fundamental (e.g. Adolph and recently Lameere) and those who ignore it. If we are right there are three fundamentally concave veins, Sc because of the basalar muscle attached indirectly to it, media from its articulation with the wing-process, and Pl, from whatever mysterious cause produced the anal furrow. There is one fundamentally convex vein, R_1 , because it carries the basal articulation with the tergum, and the residue are fundamentally neutral, but tend to become convex when they lie between two concave veins. This alternation of convex and concave veins also serves to strengthen the wing, and we believe that in the preanal region of the common ancestor of Odonata, Ephemera and Protodonata it had gone further, involving most of the wing in a system of alternate convex and concave veins. In these types we believe we can call R_{2+3} also concave, R_{4+5} convex, Cu convex and 2d Ax concave, though we are not prepared to carry these homologies over into the Neoptera as confidently. In the latter in particular we do not believe there were originally any concave axillaries, the concave folds in the axillary region lying between veins, and

only developing into I-veins secondarily. We accept the usual interpretation of other I-veins, but note that they are almost limited to the Palaeoptera.⁴

Besides the three orders which we have repeatedly mentioned, palaeontologists list several fossil types as Palaeoptera. These will be discussed more fully at the end of this paper, but we do not feel sure these are related either to each other or to the living Palaeoptera. No one has claimed that the true Palaeodictyoptera could fold their wings, — such forms as *Dictyoneura*, *Stenodictya* (Comstock Fig. 77), *Eurhythmoptyx*, Figs. 92, 100, *Hadroneura*, Fig. 96, etc. And in these types even the nymphs held their wing-pads extended straight out (Comstock, p. 92, figs. 80, 81, from Handlirsch). In these types we believe the forces narrowing the base of the wing were the same as in the Odonata, but that fusion took place independently and in a different way, — namely MA (alias R_{4+5}) fused with M, and R_{2+3} with R_1 , producing the regular series of convex veins, each with a concave posterior branch, on which Lameere puts so much weight.⁵ But we believe this state is secondary to an original condition in which only Sc and M were independent concave veins, that *Stenodictya* had never had an anal furrow, and that the slightly concave or convex condition of the anals or axillaries was due to minor causes. Whether this is due to the fact that these are the only known insects whose pupal wing pads are not folded back can only be decided when we discover the reason for the "anal furrow."

As to the higher so-called Palaedictyoptera, taking *Lamproptilia* (Fig. 9) and *Dunbaria* as examples, we find an axillary area of the Holometabolous type, fundamentally as in *Corydalid*, even to the grouping of the bases of the axillary veins in a fan. It is wholly unlikely that these could not fold their wings. Other features are also Neuropterous, e.g. the ample anal area of hind wing, and nygmata (indicated in *Dunbaria* and *Lamproptilia* by conspicuous pattern elements, though not actually reported from the fossils). The plical vein is still branched in some forms, but so is it in a few primitive Neuroptera *Planipennia*, and only the convex MA and well developed cerci⁶ show links to the true Palaeodictyoptera.

As to *Diaphanoptera* (Fig. 10) I believe it is merely a primitive relative of *Corydalid*. There is absolutely nothing incongruous, even the nygmata being shown in their proper places in Brongniart's figure. *Homaloneura* (Comstock Fig. 105) is to my eye related to it, though it still has long cerci.

Differentiation of Types of Venation

We have arrived at an insect with fully functional wings, but not yet one that can be matched by any actually known, whether living or fossil. Each of

⁴ The principal exceptions are certain cockroaches, themselves one of the most primitive groups of insects. In some Neuroptera, e.g. the Hemerobiidae, we have also the so-called trichosors; tiny bits of chitin bearing groups of sensory setae, alternating with the veins at the margin. These may also be extremely rudimentary intercalary veins.

⁵ But at least in *Stenodictya* the last of these (Cu with CuP or Pl) is followed by a purely concave vein.

⁶ A few beetle larvae still show equally well developed cerci.

the known types of wing has some further specialization, and we can cite four of these, three still living and at least one wholly fossil; typified by the Odonata, the Orthoptera, the Holometabola and (let us say) Stenodictya. In the hypothetical ancestor we had an articulation capable of movement up and down, — upwards even to the vertical position, pivoting on a longitudinal line of weakness at the base, and with some power of rotation, pivoting on a strong point formed by the junction of Radius with the tergum above and of Media with the wing-process below. Between these two joints were crowded (perhaps even crumpled) the bases of R_{2+3} and R_{4+5} , but these must have still been independent, though perhaps cut off from direct connection with the base (compare the May-Flies). Behind media again the veins must have been cut off by a flexible articular strip of membrane, through which passed blood-veins containing tracheae and nerves to supply the veins further out. The base was narrowed both in front and behind, and the most posterior veins (axillaries) and any surviving anterior ones (precostals) were gathered each into a diverging bundle. We may assume that the posterior bundle comprised a forked cubital, then a vein that was either free or already fused at its extreme base with the cubital, and behind this a homogeneous series arising from a heavy basal bar, of unknown or even indefinite number. If we forget the true Palaeodictyoptera for the moment we can say further that the wings when held vertically could be thrown back (as in resting may-flies or butterflies) and that then, at least in the hind wing two folds appeared, radiating from the articulation behind, a concave one close to the body, and a convex one through the midst of the fan of axillaries. For muscle attachment and to govern the various motions there was a system of so-called basal sclerites: and the following, which are shared by may-flies and higher insects, must be credited to the archetype. Below the wing there were two sclerites (originally cut off from the episternum and epimeron), the basalar before the wing-process and the subalar behind, each bearing the insertion of the corresponding "direct wing-muscle" and connected by strengthened membrane to subcosta and the cubito-axillary group of veins respectively. On the dorsal side it is not so clear, but it would appear that the membranous line forming the joint fell farther in than the point of articulation of the wing to the pleura, and that this overlapping portion contained swollen and distorted bases of the main veins (at least radius and one more, and the common base of the axillary mass) which served as the attachment of the muscles that lifted the wings. This is still essentially the state in the Odonata. Between the second and third was a plate of lighter chitinization, doubtless representing the vestige of the base of media, perhaps combined with what later became Rs. This plate is the median sclerite; it folds diagonally in the middle when the wing is folded back, even in *Siphonurus*.

From this point on we must follow several lines of evolution separately. What we have just described is practically the condition in the primitive may-fly, *Siphonurus*.

Palaeoptera

In the early twenties it gradually became evident that the may-flies and dragon flies stood in contrast to other living orders of insects, and this condi-

tion was put on record in 1924, independently by Martynov in Russia⁷ and by Crampton.⁸ I am not sure which name has priority, but will accept Martynov's since it is simpler and equally appropriate. Each proposed the term to include the insects known (living) or believed (fossil) to be unable to fold the wings back over the abdomen. For the latter they chose secondary evidence differently, Martynov emphasizing the arrangement of the anal-axillary veins and Crampton the basal sclerites. In fact both characters break down, and we will use the term in a more restricted sense, basing it partly on other characters.

We will limit the term Palaeoptera to the Ephemera and Odonata with their fossil kin, chiefly the Protodonata. They show the following characters, most of which have occasional exceptions on one side of the line or the other: Wings without basal sclerites dorsally (vestigial in lower Ephemera and presumably present in fossil types), not capable of being folded back rooflike over the abdomen (so folded in nymphs of Ephemera and perhaps ancestrally in the adults); wings generally plaited in a characteristic way, with four special *crucial plaits* (see below); costal space with true cross veins instead of veinlets branching off Sc and R₁; wing of imago not bearing setae (but with marginal setae in subimago of Ephemera); R₁ wholly free and unbranched;⁹ 2d Ax a concave vein. In the living species there are always triangular brace-veins near base of wings, crossing from costal edge to R, but these are not always visible in fossils.

The fluting of the wing-membrane reaches an extreme in the may-flies and Protodonata, where practically every vein and branch enters the fluting system, and practically every fork of a vein contains a prompt second fork or intercalary vein of opposite sign.

In particular note what I shall refer to as the four *crucial plaits* (stippled in the figures): — in these cases two veins of opposite sign run closely parallel for a distance, with usually only a single series of cells between them, and one or both giving off a series of branchlets on the other side; these are (as I interpret the venation, see below): R₁ and the serial Rs—R₂, the serial R₂₊₃&R₃ and R₄₊₅&R₄; M₃₊₄ and Cu&Cu₁; Pl and 1st Ax. These occur identically in Odonata, Protodonata and the earlier Ephemera (Protereisma) though in some later Ephemerids the number of intervening rows of cells is increased, but are absent in forms with much reduced venation, such as Zygoptera, the highest may-flies, and Ditaxineura.

Another character that both may-flies and dragon-flies have in common,

7 Rev. Russe Ent. 18, 145-174, 1924, translated in Psyche 37, 245-280, 1930; Zeit. Morph. Ök. Tiere 4, 465-501, 1925. He proposes the name Palaeoptera (misprinted Paleoptera in the translation).

8 Jour. Ent. Zool. 16, 33, 1924. He proposes the name Archipterygota.

9 The figures in Needham's "Biology of May-Flies" show Rs stalked with R₁ on the hind wing, but all the specimens of fully veined may-flies examined show them completely separated. In Siphonurus there is actually a slender clear space between them. In the Odonata all species examined show them separate, while practically all figures published show them fused.

but which is not strictly limited to them, is the extremely smooth wing-membrane, with neither fixed hairs nor setae; but if we can trust the preservation of our fossils, some of the types related to the *Anisaxia* also show the character. I have not seen it in any other living form, though often setae are limited to the veins and margins and very minute. And these two orders agree, and differ from other types of insects, in the nymphs being highly specialized for aquatic life and far different from the adult. In all early aquatic Neoptera the nymph is fundamentally much like the adult, and has probably been in the water for a much shorter period.

Enough of these characters mentioned are definite specializations so that we must assume these two Palaeopterous orders, with their fossil kin, have had a common stem, though certainly they had already separated when our fossil record begins. Beyond this point we must consider them separately.

Ephemerida

It is quite impossible to determine which is more primitive, the Ephemerida or the Odonata. Each has unique primitive features, and each shows not only its own specializations, but features suggestive of higher forms, though on the whole the may-flies have the more of both.

As primitive features we may just mention the paired reproductive outlets, presence of two winged instars, free though minute terminal segment of the larval mandible (the so-called lacinia), and in the wing the presence of more than three axillary veins (in a few of the lowest types) the 4th as well as the second being concave. Most striking of all is that the veins which make up Rs, M and Cu in higher forms are still a floating fan-like mass, — though they have lost their bases, they have not yet joined up with R_1 . There is definitely no MA of Lameere, since the convex R_{4+5} while free from the base of R has already joined with R_{2+3} .

The only feature that definitely connects with Neoptera is the presence of the complete set of basal sclerites in primitive types, though no may-fly is known to fold its wings roof-like, and perhaps the gathering of the axillary branches on a basal transverse chitinization (emphasized as a black bar in the figures).

To derive this scheme from the general Palaeopteran type we need only this gathering of axillaries, for the joining of R_{4+5} (MA) to R_{2+3} , and the limiting of terminal branching to certain fields, leaving the four crucial plaits free, are shared by the Odonata, and therefore already Palaeopteran.

In the two figures, one of the hind wing of the fossil *Protereisma*, the other of the primitive modern *Siphonurus*, I have emphasized the four triradii and the crucial folds for easier comparison, but it is easy to see they are almost identical, even to the pectinate Cu_1 .

The history of the Ephemerida begins in the Permian, and we have no idea what may have lain behind them. *Triplosoba* (known by a single specimen) has been suggested as the ancestor, but its venation is of quite a different

type with simple MA out of the stem of M, R_1 already stalked on R_s , and quite different cubito-axillary system. It certainly belongs in the company of Palaeodictyoptera.

Protodonata and Odonata

Comparative Nomenclature of Venations

Present Scheme	Comstock-Needham * <i>Bases</i>	Tillyard (later)**
C	C	C
Sc	Sc	Sc
R_1		
$R_s + M + Cu$ }	$R + M$	$R + M$
PI †	$Cu + A$	$Cu_2 + 1A$
Ax	$A' \& A \ddagger$	$A' \& A$
<i>Terminations</i>		
C	C	C
Sc	Sc	Sc
R_1	R_1	R_1
R_2	M_1	R_2
R_3	M_2	R_3
R_4	R_s	IR_3
R_5	‡	
M	M_3	R_{4+5}
Cu_1	M_4	MA
Cu_2	‡	
PI †	Cu	Cu_2
1Ax ††	Cu	1A
1Ax _a	A_1	‡
2Ax	§	Aspl
3Ax ₁	A_2	‡

* As given in the "Wings of Insects."

** As given in the "Insects of Australia and New Zealand."

† Note that the designations PI of my system, CuP of Lameere and Cu_2 of Neuropterists are concededly merely different designations of the same veins.

†† Not so labelled, but basal part shown (in black) as a cross-vein.

‡ Obscure veins, usually broken up where the supplements cross them, figured but not named by Comstock-Needham *et al.*

‡‡ Reviving the term "Axillary" for the veins often called "anal" but distinct from the original anal vein (which was usually PI of my system).

§ Absent in forms figured.

VARIANT SYSTEMS: *Ris* considers the bisector of the anal loop (my 2 Ax) a true vein, labelling my 1Ax, 2Ax and 3Ax, A_1 , A_2 and A_3 respectively. He also accepts the whole base of this stem as a true vein (A).

Tillyard in earlier papers follows Comstock, except that he counts Comstock's R_s as a secondary branch of M, labelling it Ms and later IR_3 .

Carpenter follows *Tillyard's* later system, except that he accepts *Tillyard's* IR_3 as the true R_3 .

Handlirsch follows *Comstock* in the Odonata, but in the Protodonata he only marks main vein-areas, assigning C, Sc, R, as I do, assigning both my M and Cu to M, Pl and 1Ax to Cu, and 2Ax and 3Ax to A, — with no attention to basal connections.

All workers except *Comstock* and *Tillyard* (after his earliest papers) consider the roundabout course of the anal trachea as secondary; they treat the apparent base of A as its base and the "anal crossing" as merely a modified cross-vein.

In the Protodonata and Odonata the crux is the interpretation of the venation. I have assumed that the tracheation is more plastic than the venation, as in other orders, and as would be expected from the less precise adjustment biologically necessary. So I have accepted the so-called "radial sector" as a purely tracheal modification, and treat the vein which it occupies (being the first convex one of the sectorial area) as R_4 , as in all other orders with well differentiated convex and concave veins, — in this I follow *Tillyard*; but I also accept the anal tracheation as secondary (as *Tillyard* has shown, it varies from genus to genus) and so follow *Needham* in viewing the 'anal crossing' as a cross-vein only secondarily occupied by a trachea.

I have interpreted the whole system on the assumption that the plaiting is fixed in these strongly plaited forms, and in particular that the four crucial plaits (stippled) are homologous with those of the may-flies, — like them, the first is convex before concave, the other three concave before convex; and the last one, alike in Ephemerida, Protodonata, and Zygoptera and Anisozygoptera, is doubly sinuate in the same way.

None of the living Odonata and Ephemerida can fold the wings back, but this character is weakened by the presence of the axillary sclerites in some Ephemerida, our lack of knowledge in the case of fossil types, and the reappearance of the same character as a degeneration in many Lepidoptera.

Against the features which show plainly a common ancestry for the three orders we have the fact that there is no convergence between them in the fossil record, and that Odonata and Ephemerida each have primitive features not shared by the others: the Odonata having only direct wing-muscles, and no trace of the dorsal axillary sclerites as separate elements.

To derive the Protodonata from the common Palaeopteran we must add the following specializations: wing much narrowed, the main veins running roughly parallel, M and Cu fused at base with Rs (though *not* with R_1 !); the three anals fused though each with a separate system of terminal branching; the more basal branches of the third with any surviving more posterior axillaries appearing as parallel posterior branches of the main stem: M reduced to a simple vein. The family figured (*Meganeuridae*) and most forms known show

a tendency to reduction of the apical part of wing, reaching an extreme in *Paralogus*, but only slight in *Protagrion*.

To derive the Odonata only moderate further modifications are necessary, mainly the forming of the nodus by the development of a strong cross vein at tip of Sc, and a definite stigma. The other features generally thought of as Odonate appear within the history of the Order. The Mesozoic *Aeschnidiopsis*¹⁰ (Fig. 8) does not yet have an arculus, but only a sharp bend in Cu at the proper point, and still has a dozen free posterior branches of the anal stem. Unfortunately the anal loop area is lost, but *Aeschnidium*¹¹ shows the same condition as in the Meganeuridae, — a moderately branched 2d Ax as well as 1st Ax; though in this genus a secondary vein has developed parallel to the base of Ax (obviously an 'anal supplement') cutting off the bases of the axillary branches, just as the R and Cu supplements often cut off the bases of their respective branch veins.

As to the further development of the anal loop, *Synthemis* shows the exact condition of *Aeschnidium*, and the rest of the Macromiinae and Aeschnids could easily come from it by reduction, but the true Libellulinae come much closer to the true Protodonates, and presumably to the unrecorded condition of *Aeschnidiopsis*, for their "boot" could be derived directly from the Meganeurid merely by the reduction of 2 Ax to a single vein and resulting convergence at the margin of branches of 1 Ax and 3 Ax, as suggested in the figures. It is interesting to note that a few genera (possibly degenerate) do not have this convergence, though the bisector of the loop (i.e. 2Ax) is always simple. The best developed of these are *Nannothemis* and a few relatives, which also do not yet have the "triangle"; in *Bironides* and *Tetrathemis* the veins which are to become arculus and triangle are still three ordinary cross-veins.

Note also that in the Zygoptera and Anisozygoptera (both fossil and living) the structures that are to be the triangle, subtriangle and supertriangle remain ordinary cells, and the corresponding junction of Pl and Ax does not take place, but we have two parallel sinuous veins to bound the fourth crucial plait just as in the Protodonata.

In all living Odonata the anal area is much reduced, the Anisoptera with one to at most three (*Tamea*) free posterior branches, and the Zygoptera with mere stubs, but the Aeschnidiidae of the Mesozoic still had a good number (7 in *Aeschnidium*, 12 in *Aeschnidiopsis*). *Agriion* has the most of any living Odonata (apparently toward a dozen) but is believed to have a secondary increase in the number of veins generally.

Practically all the fossils that may belong to this series are recognized Ephemerida, Protodonata or Odonata. The only exception is *Ditaxineura*, which still has the oblique costal brace of the Ephemerida with the wing form of the Odonata and reduced venation. The separate *R*₁ is obvious in all fossils actually examined, though often not figured, and all other types sometimes called Palaeoptera are excluded by this character.

10 See Tillyard, Proc. Linn. Soc. N.S.W. xlii, Pls. 42, 43, 1917.

11 See Handlirsch, Foss. Ins. pl. 47 fig. 16, 1908.

Palaeodictyoptera

There is a complex of types, all fossil, in which both radius and media are formed of a convex anterior and a concave posterior branch. I believe these are separately derived from our hypothetical type by the junction of the potential R_{2+3} to R_1 , making its concave posterior branch, but of the next (convex) R_{4+5} to the following medial stem, to which it gives a convex anterior branch. I do not agree with Lameere that this is a primitive condition, or one from which the living Hemimetabola are descended (as to the Holometabola, see further). It represents approximately the Palaeodictyoptera of Handlirsch, but within the long series of families we have two distinct types, which I believe should stand as separate orders. The true Palaeodictyoptera are marked by a nymph with the wing-pads extending directly out, unlike all other insects (Wings of Insects, Fig. 80), simple convex media anterior, rarely forked close to the margin, and then much less richly than the concave media posterior or true media; simple or rarely two-branched Cu (anterior) with a more richly branched CuP (not developed as a plical) attached to its posterior side; first axillary vein (in Stenodictya) also concave, but widely separated from CuP, the following ones apparently convex; but none of the plaiting as well marked as in the preceding orders, only Sc being really deeply concave. There is no evidence that this series ever folded their wings, and the hind wings have the same simple series of anals as the fore, so far as preserved, with no grouping in an anal fan. The nymphs have been assumed to be aquatic, but I think on no evidence whatever.

This series is characterized from Stenodictya, the only type on which I have seen evidence of the convexity and concavity of the veins. It will include the whole Dictyonauridae as limited by Handlirsch (these being the original Palaeodictyoptera of Goldenberg), also Peromaptera, Megaptilus, Hypermegethes, Mecynoptera, the Lithomantidae, Lycocercus, the Homiopteridae, etc., in Handlirsch's series to Spiloptilus, inclusive, but excluding Fouquea, and finally Polycyagra. The only divergence, except for varying degree of imperfection of the record is in a few genera where Cu becomes (or remains) more richly branched, particularly Mecynoptera, Heolus and some Homiopteridae. I have seen no evidence on the plaiting of these types, but the sparse and rather evenly spaced axillaries of these are still of the Stenodictya type.

This series contrasts with the Palaeoptera, with which they have been associated, in the stalking of R_{2+3} on R_1 , presence of costal veinlets, narrow plaits with a convex in front of a concave vein (unlike the crucial plaits of the Palaeoptera), and much less defined plaiting generally, lack of a definite plical vein, the concave vein on the posterior side of Cu being an ordinary branched vein, and followed (in Stenodictya at least) with a second but widely spaced concave vein and then a convex one. They differ from these and from all living insects as well in the absence of a posterior convex branch of Rs, with correlatively the presence of a convex anterior branch of M, and the nymph with wing pads sticking straight laterally. Obviously they must have been derived from a separate line far before our fossil record begins, and

the evidence is on the whole that they have left no descendants. Eubleptus and Eugeneon have all the essential features of this group, and Triposoba shows the characteristic simple MA. They should not be associated with the Hemiptera or the Ephemera.

Orthopteroidea

The great majority of the remaining living Hemimetabolous insects have another definite type of wing. The fluting is less definite than in the Palaeoptera, and tends to fade out, though in this case it is Sc rather than Pl which tends to lose its concavity. On the fore wing M is easily identified from the under face of the wing, but on the upper side is sunk into a sharp depression, that most often closes over as a deep fold, typically covering the bases of all the veins from M to Pl (2 Pl in this series). The cockroaches and most Orthoptera have the closed fold, the Gryllacrididae, Plecoptera and Hemiptera have the open groove, but in the latter an axillary sclerite slips into it and fills it in the folded position. In this series R_{4+5} is fundamentally a portion of radius, which shows a convex posterior branch whenever the plaiting is recognizable in the outer part of the wing, and M is wholly concave, so we judge that we again have a distinct way of grouping the original veins into a definitive pattern: $R_1 : R_s : MP$ in the Palaeoptera; $R_{1-3} : MA+MP$ in the Palaeodictyoptera; $R_{1-5} : MP$ in the Orthopteroids. Another unique feature is the anal furrow: in all the forms with fairly complete venation there are two plical veins, i.e. besides the concave vein which normally appears as a basal posterior branch of Cu, there is a second independent concave vein in the anal furrow, which I will call 2 Pl, before we come to the first member of the true axillary series. The hind wing lacks the basal furrow or fold but has the second plical, — in fact in the cockroaches there is even a third plical, which comes out of the base of the axillary system, but is plainly of a different kind from the usually branched true first axillary.

This venation pattern obviously includes the Plecoptera and the Hemiptera as well as the Orthoptera in the broadest sense, and like the two preceding types is distinct from the beginning of our fossil record. Whether it also includes the Psocidae and their kin does not appear from wing-characters: the Psocids lack the basal fold and the second plical vein, which would seem to favor the stem of the Holometabola, but the venation is too reduced to make the connection compelling. On the other hand the incomplete transformation is against this, though the ancestors of the Holometabola must have had it once, the body characters are generally considered Orthopteroid, and the oldest recognized fossils look almost exactly like Homoptera of the same period, until we note the position of the base of Cu. In the Psocidae there is a wide space between Cu and the common stem of R and M, filled with flat membrane, in the more reduced Homoptera the basal fold brings them in contact, and then in the Psyllidae and probably the Archescytinidae they actually fuse. In the Homoptera the two plicals fuse in the fore wing at the same stage (between the Auchenorrhyncha and Sternorrhyncha), whereas there is only a single weak (first) plical in even the most primitive Psocidae.

Holometabola

In placing the Holometabola we are faced with a dilemma, which the known fossil record cannot clear. At first glance the grouping of radial veins is just as in the Orthopteroids, and the fate of the second (and possibly third) plical could be easily explained by comparison of the Trichoptera with the Plecoptera (Forbes, 5th Ent. Congress, p. 282, 1933). Also the folding of the wings is exactly the same, even to the detailed way in which the axillary sclerites work (see Snodgrass, Principles of Ins. Morph. 215 ff.). But the fossil record seems to show a different connection, from the Palaeodictyoptera, through a series of annectant types to the true Neuroptera, by a late transfer of MA to the radial stem, — in fact many Neuroptera still have a slanting vein out of the base of M running across to the base of R or Rs (r-m of recent authors), plainest in the hind wing.

We must now bring up a series of fossils which have been grouped with the Palaeodictyoptera, but show all but one of the characters of the Holometabola, and to emphasize their fundamental importance I indicate for them a new Order:

Anisaxia, new order

Insects with so far as known the general body type of the Palaeodictyoptera, with ample wings, slender body and long many-segmented cerci. Wings with radial sector wholly concave, media with a several-branched anterior convex branch (MA), Cu also several-branched, the concave posterior fork (CuP or 1 Pl) not more richly branched and often simple; following vein a true axillary, convex and normally branched, often pectinately, the following axillaries (usually imperfectly preserved) more crowded, and in the few cases visible arising from a transverse basal bar, as in all richly veined types which fold their wings. Hind wing noticeably broader than fore wing, especially toward inner margin.

This group differs from the Palaeodictyoptera in having richly branched anterior forks on both M and Cu (i.e. MA and true Cu) and especially in having all the signs of true wing-folding, the proportions being about as in the *Corydalid* group, with true anal furrow and associated plical vein. It differs from the true Holometabola in having long multisegmented cerci, and a convex MA attached to M and not to Rs. The nymph is unknown, but we may guess that the wing-pads were folded back and down as in Holometabolous pupae. It is also natural to assume that the transformation was incomplete and the nymph aquatic, but our evidence is nil. It would appear that the modern Neuroptera have been derived from it by two separate stems, since the *Myrmeleonid* shows a several-branched Pl¹² (as in *Lamproptilia*, *Compsoptera* and *Homaloneurina*) while the Megaloptera like all other Holometabola have a simple one like *Spilaptera* and *Dunbaria*.

This order will contain Handlirsch's *Spilapteridae* (including *Dunbaria*)

¹² Best shown on the fore wing of *Palpares*.

and Lamproptilia. Fouquea is not completely enough known to place for certain, but also appears to belong here.

A feature of several orders of Holometabola, but of no other insects is the presence of nygmata (Forbes, Ent. News xxxv, 230, 1924). These are not generally shown in figures of fossils, but the pattern of Lamproptilia (Fig. 9) strongly suggests their presence. In Diaphanoptera (Fig. 10), which Handlirsch would make a separate order related to this series, they are plain, but I believe Diaphanoptera is merely a primitive genus close to Corydalid.

The Megasecaptera show the same body type, though with much reduced venation, eliminating most of the distinctions between the Palaeodictyoptera and Anisaxia; but the fact that at least Asthenohymen folded its wings points strongly to the latter. The names "Protohymen" and "Protohymenoptera," applied to a section of this order, are based on a superficial resemblance that has no basis in more important features.

Summary

1. Wings arose in insects as extensions of the lateral edges of the terga.
2. Flight developed in 4 stages: *a*, leaping, *b*, gliding, *c*, steering, *d*, true flight.
3. The "direct" wing muscles are more immediately adapted for flight than the "indirect" ones, and probably gained their function first.
4. The adaptations in structure of the wings were: *a*, extension in length, perpendicular to the body, *b*, moving forward of the ventral pivot (top of pleural suture) *c*, crowding of anterior veins (C to M), *d*, thinning of wing substance to membrane, with closure of its cavities except at veins for support and blood supply, *e*, formation of a hinge by *f*, loss of chitination of bases of veins, and *g*, narrowing of base with resulting crowding of vein-bases.
5. The narrowing of the wing-base resulted in basal fusion of neighboring veins (and their tracheae).
6. This fusion in the radial region took place in three different ways: *a*, R_1 (convex) free, R_{2+3} (concave) fused with R_{4+5} (convex); *b*, R_1 fusing with R_{2+3} , R_{4+5} fusing with M (concave); *c*, R_{2-5} fusing with R_1 at base, M (concave) free.
7. These three types of reduction of the wing base represent three lines which separated before the beginning of our fossil record: Palaeoptera, Orthopteroidea, Palaeodictyoptera.
8. The Holometabola make a fourth group older than our record, but could have been derived from either Orthopteroidea or the Palaeodictyoptera.
9. The Psocidae and their kin are similarly ambiguous and may be related to the Holometabola. They lack two distinctive features of the Orthopteroidea: the groove at base of fore wing and the second plical vein.
10. The principal orders of winged insects fall into these groups as follows:

- a, *Palaeoptera*: Ephemera, Protodonata, Odonata.
- b, *Orthopteroidea*: Orthoptera, Dermaptera, Plecoptera, Hemiptera.
- c, *Palaeodictyoptera*: (restricted), with Protephemera and Protohemiptera.
- d, *Psocoptera*, perhaps with Parasitica and Thysanoptera.
- e, *Holometabola*: Anisaxia (now separated from Palaeodictyoptera), Megasecaptera (with Protohymenoptera), Neuroptera (with Diaphanopteroidea), Coleoptera, Hymenoptera, Mecoptera, Diptera, Trichoptera, Lepidoptera.

NOTES ON FIGURES

Fig. 1. is hypothetical, drawn and lettered to be comparable to Snodgrass: "Principles of Insect Morphology" fig. 96.

Figs. 4-7. Slightly diagrammatic and partly composite. The "crucial folds" are emphasized by stippling, and the four most important triradii of the may-flies by thickening the bases of the veins.

Figs. 4 and 6 after figures by Carpenter.

Fig. 8. mostly after Tillyard, in Proc. Linn. Soc. N.S.W. xlii, pls. 42, 43, 1917, completed where broken from *Aeschnidium densum* Hagen, Handlirsch "Die Fossilen Insekten" pl. 47, fig. 16, 1908. Most crossveins omitted and crucial plaits stippled.

Figs. 9 and 10 after Brongniart, somewhat simplified; the markings indicating position of nygmata in Fig. 9 and nygmata in Fig. 10 accented.

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Effects of Burning-over and Raking-off Litter on Certain Soil Animals in the Duke Forest

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Introduction

Denudation of soil by removal of litter that has been formed as a result of accumulation of fallen leaves and other organic materials is well known to produce significant changes that affect growth of trees. Not only is much of the organic matter removed and available nitrogen decreased, but soil also tends to become more alkaline (Jenny 1941) and without a humus layer may tend to form superficial crusts (Hilgard 1930). Burning-over releases mineral salts; thus makes a soil surface more alkaline and also opens the way to loss of salts by leaching (Issac & Hopkins 1937). Cultivation tends to decrease nitrogen; it makes particles smaller and soil more compact. The removal of litter and humus decreases water-holding capacity and soil erosion often results. Rains drive air out of soils and, if there is no humus or litter to shelter soil animals, they are exposed to enemies and other dangers (Shelford 1929).

In 1936 Dean C. F. Korstian, Duke University, School of Forestry, proposed a cooperative project to investigate the effects of denudation on certain areas in the Duke Forest. In 1934 three 0.1-acre plots had been surveyed and set aside for experimental purposes. All were quite similar, on a gently-sloping hill side, and were covered by a stand of loblolly pine (*Pinus taeda* L.) that in 1934 was 31 years old. One of the plots (No. 31) was burned over at intervals, one (32) was left intact, and on a third (33) all logs and fallen trees were removed and litter was raked off so as to leave the soil perfectly bare. Dr. Korstian and other members of the School of Forestry measured and numbered all trees and made maps showing distribution; Drs. H. L. Blomquist and H. J. Oosting undertook the study of plants that made up the rather scanty ground cover; Dr. T. S. Coile studied soils; and the writer made routine observations on macroscopic animals present in litter and soil. Plot 31 was burned over on the following dates: October 6, 1936; May 11, 1937; May 12, 1939, and May 1, 1941. Plot 33 was cleared and raked: October 19-24, 1936; April 23-28, 1937; May 17, 1939; May 1-3, 1941. Korstian & Coile (1938) have given a complete account of type of soil, particle size, moisture content, distribution and size of roots, and other matters relating to the plots. Concerning the soil on the areas studied they say:

Alamance soil is derived from fine-textured basic metamorphic rocks of the Carolina Slate Formation. It is often shallow, and frequently a B. horizon is not present. The soil profile. . . may be described as follows:

A₁ horizon. 0 to 1 inch. Dark gray friable loam.

A₂ horizon. 1 to 5 inches. Light gray to almost white floury stony loam.

B₁ horizon. 5 to 15 inches. Yellow friable stony clay.

B₂ horizon. 15 to 21 inches. Yellow friable clay.

C horizon. 21+ inches. Yellow, gray, and reddish rotten rock.

The more shallow phases of Alamance soil represent relatively severe conditions for tree growth during periods in the growing season when precipitation is deficient and temperatures are high. Roots do not penetrate the soil to great depth and water percolation through the profile is impeded by the impervious nature of the B horizon. The occurrence of relatively large amounts of material larger than 2 mm. in diameter (stone) in the surface soil is an erosional feature and further evidence of the absence of good percolation.

The many animals that live in forest litters and soils make essential contributions to such habitats and improve conditions for the growth of trees. They turn over and aerate soils (Darwin 1890, Bornebusch 1930, 1940, Branner 1912, Taylor 1928), and increase availability of minerals and other plant foods (Bornebusch 1940, Eaton & Chandler 1942, Green & Reynard 1937, Hilgard 1930, Varga 1937, Waksman 1932).

In order to compare the faunas of the two denuded plots (31, 33) and the control plot (32), collections were made every three months for five years, 1937-1941. On each area 36 square feet were examined. Before each collection temperatures were taken at the surface of litter and at a depth of three inches in soil. A 3 by 6 ft. waterproof canvas blanket was then spread on the ground. In a band 18 in. wide around this the litter was scraped up and sorted over a little at a time on the blanket. All animals found were recorded and preserved for identification. After the litter had been thoroughly examined and piled at one side, the soil on the area from which it had been removed was dug up to a depth of three inches with a mattock. The soil was then sorted over with a trowel and any animals found were preserved. In preliminary observations before the routine study of the denuded plots began, digging was carried to a depth of six inches; but, as soil was very dense and was found to harbor few or no animals below three inches, most of the later observations did not go deeper. By the methods described 36 sq. ft. of litter and the same amount of soil to a depth of three inches was thus examined every three months.

The writer's thanks are due to C. F. Korstian, Wm. Maughan, and T. S. Coile who helped with advice and in other ways; to George W. Wharton for help in sorting and identifying specimens; and to various specialists who identified animals and to whom acknowledgements are made in appropriate places in the list of animals of the Duke Forest that comes later in this paper.

Temperatures

Each time before collections were made temperatures were taken in the shade on the surface of litter and at a depth of three inches in soil. The results are shown in Table 1. The undisturbed plot (32) showed the greatest stability (least "extreme range") both on litter surface and in soil. The burned over plot (31) was not very different from the raked one (33); it showed a wider range of surface temperatures but a more limited range in soil. The difference

TABLE 1.—Temperature (°C.) in Duke Forest on surface of litter and at depth of 3 inches in soil.

Date	Weather	Plot 31			Plot 32			Plot 33		
		Time A. M.	Surf.	3 in.	Time A. M.	Surf.	3 in.	Time A. M.	Surf.	3 in.
March 7, 1937	Clear	8.05	9.2	8.8	9.50	14	8.8	11.55	14.8	9.2
March 27, 1938	Cloudy	10.50	14.8	11.8	8.50	12.5	11.6	7.35	11.0	11.0
April 2, 1939	Cloudy	11.45	14.8	9.8	9.35	12.0	9.2	8.03	8.0	8.4
April 3, 1940	Cloudy	9.58	14.0	10.0	8.42	12.3	10.2	7.45	13.0	9.9
April 6, 1941	Sun; wind	9.50	13.6	9.8	6.48	10.0	8.1	8.33	9.7	8.0
Average			13.3	10.0		12.2	9.6		11.3	9.3
Range				3.3			2.6			2.0
June 20, 1937	Clear	8.00	22.3	20.9	8.20	24.6	21.8	10.15	25.3	22.7
May 29, 1938	Wet, partly cloudy	10.50	19.5	18.2	8.20	19.0	17.2	6.50	17.0	16.8
May 28, 1939	Clear; dry	11.05	30.4	21.5	9.20	24.3	18.7	7.58	21.7	19.5
June 30, 1940	Clear; dry	6.25	16.0	18.7	7.20	16.3	17.2	8.35	17.6	18.6
May 18, 1941	Clear	8.35	13.6	14.5	7.28	10.8	13.3	6.40	10.1	13.4
Average			20.4	18.8		19.0	17.6		18.3	18.2
Range				1.6			1.4			0.1
Sept. 25, 1937	Clear; dry	3.23*	23.3	18.9	1.24*	24.4	18.0	12.08*	24.0	18.5
Oct. 2, 1938	Clear	10.20	13.8	14.2	8.45	12.4	15.0	7.37	12.0	13.9
Sept. 17, 1939	Clear; dry	7.20	21.0	20.6	8.20	21.3	19.6	10.10	24.7	22.5
Oct. 6, 1940	Partly Cloudy	10.10	18.6	15.0	8.35	14.0	14.3	7.20	13.0	15.0
Sept. 28, 1941	Misty	9.20	20.0	17.7	7.10	15.7	16.8	6.00	14.5	15.8
Average			19.3	17.3		17.4	16.7		17.6	17.1
Range				2.0			0.7			0.5
Dec. 26, 1937	Clear; wet	11.15	8.2	6.3	9.40	6.1	6.7	8.16	5.1	5.1
Jan. 3, 1939	Clear	8.30	1.0	4.2	10.20	6.6	4.5	12.30*	11.0	4.7
Dec. 23, 1940	Clear; wet	8.25	4.0	5.2	10.44	4.8	5.6	9.44	4.2	4.8
Jan. 7, 1942	Cloudy	9.27	-3.3	-0.3	8.23	-4.6	3.5	7.45	-5.2	0.0
Average			2.5	3.9		3.2	5.1		3.8	3.9
Range				1.4			1.9			0.1
Grand Average			13.9	12.5		13.0	12.3		12.8	12.1
Grand Average Range				2.1			1.7			0.7
Extreme Range			33.7	21.8		20.0	18.3		29.9	22.7

between surface and soil in the same locality was in general greatest in the burned area (2.1°C.) least in the raked area (0.7°C.). This may be taken to indicate that the charred logs and rain-washed windrows of litter afforded some degree of insulation to the soil below, but temperatures in the raked area had no such protection against variations. The thick layer of loose litter on the undisturbed plot (32) appeared at times to be less effective as a thermal blanket than the compact litter on the burned area (31). However, in extreme cold weather (January 7, 1942) soil in the undisturbed plot (32) remained well above freezing temperatures (3.5°C.), whereas that in the other two did not ($-0.3, 0.0^{\circ}\text{C.}$). Also, on a very hot day (May 28, 1929) the undisturbed plot did not reach as high a soil temperature, (18.7°C.) as the other two, though one of these was observed earlier (19.5°C.) and the other later (21.5°C.) on the same day.

The data in Table 1, though quite limited, indicate that complete or partial removal of litter by raking or burning made the soil, as a habitat for animals, subject to more extreme temperatures. This was also doubtless accompanied by greater exposure to desiccation, which was perhaps more significant for litter and soil animals than temperature variations. When Dr. T. S. Coile has completed his studies on the plots under discussion, he will publish data on the water content of soils, pH, particle size, etc.

Distribution of Litter and Soil Animals

Table 2 shows the numbers of the most common animals collected on nineteen different days from the three types of plots, 1937-1941. Table 3 summarizes the total numbers of all animals collected on various dates. The distribution of various more or less common animals will now be considered. Those that seldom occurred will be found in the list that makes up the next section of this paper.

Earthworms.—Although several species occur in and near the forest, only three were found on the three plots studied in connection with denudiation. Table 4 shows that nearly twice as many were collected from Plot 32 as from the other two together. Large, stocky *Eisenias* were clearly most common on Plot 32; slender *Diplocardias* were rather evenly distributed on all plots, but somewhat scarcer on 31; little *Bimasti* were rare and slightly more abundant on 32. Both *Eisenias* and *Diplocardias* were most abundant in spring (Fig. 1). During dry periods they perhaps sought shelter under the bases of trees or in other situations. No indication was seen that they migrated to deeper levels in the hard, closely packed soil.

Centipedes and Millipedes.—Centipedes were more numerous in litter than in the soil beneath (Table 5). They were twice as abundant on Plot 32 as on the other two combined; there were twice as many on the burned area (31) as on the raked area (33). Millipedes were collected about as often on the raked plot (33) as on the one left intact (32), but only a fourth as many occurred on the burned area (31). Both types of myriapods showed a tendency to go

from litter into soil during cold or dry periods. On the raked area there was a preponderance of millipedes in soil; this was due to the occurrence of 12 individuals in one collection on December 26, 1938; after that date none was seen on the area. In general the number of myriapods was too limited to be significant as evidence of seasonal migrations.

Beetles.—In soil more scarabaeid larvae were collected in denuded plots than in the undisturbed area (31-18, 32-12, 33-17), but in litter the opposite was true (31-2, 32-4; 33-1). Adult scarabaeids were most common in the litter of the undisturbed area (31-5, 32-17, 33-1); only one larva was found in litter in Plot 32. Elaterid and tenebrionid larvae and various small beetles were also most prevalent in Plot 32 (Table 2).

Ants.—Several species were found. Collections gave the following numbers of individuals: 3 (0.1%) in winter, 276 (17%) in spring, 1000 (62%) in summer, and 330 (21%) in autumn. Distribution is shown in Table 6. Two-

TABLE 2.—Total number of most common types of animals collected on nineteen days, 1937-1941.

	31-burned	32-intact	33-raked
Earthworms			
Eisenia	54	134	22
Diplocardia	79	124	130
Bimastus	1	1	0
Centipedes			
Litter	14	46	7
Soil	9	22	5
Millipedes			
Litter	3	13	1
Soil	1	2	15
Small Beetles	4	87	18
Ant guest beetle	1	92	
Scarabaeids			
Soil			
Larvae	18	12	17
Imagoes	2	4	1
Litter			
Larvae	5	17	1
Imagoes	0	1	0
Tenebrionid & elaterid larvae.....	10	19	4
Diptera larvae	12	11	6
Cockroach	12	31	16
Cricket	3	4	1
Ants	326	1086	189
Machilis	2	8	5
Mites	2	23	3
Spiders	58	124	25
Rabbit feces	2	8	4
Rodent burrow		1	1

TABLE 3.—Total number of animals collected.

	31-burned		32-intact		33-raked	
	Litter	Soil	Litter	Soil	Litter	Soil
March 7, 1937	7	26	12	30	2	19
June 20,	241	22	655	1	29	83
September 25,	9	1	124	7	26	154
December 26,	16	0	18	12	3	42
March 27, 1938	2	8	96	78	0	24
May 29,	103	4	236	34	9	27
October 2,	27	5	14	4	5	7
January 3, 1939	5	17	14	16	2	5
April 2,	21	42	107	173	3	33
May 28,	22	6	25	125	14	55
September 17,	5	1	146	19	5	1
April 3, 1940	7	26	15	27	1	14
June 30,	4	0	55	2	16	50
October 6,	60	13	45	9	19	8
December 23,	1	23	7	16	2	12
April 6, 1941	116	8	26	14	8	33
May 18,	2	6	4	2	1	0
September 28,	11	0	76	23	4	1
January 7, 1942	0	0	0	11	0	1
Frequency	18	15	18	19	17	18
Total No.	659	208	1675	603	149	569
Per cent	75.9	24.1	73.5	26.5	20.7	79.3
Total Number	867		2278		718	
Per cent	22.5		59.0		18.5	

thirds were found in the intact area (32) and only a little more than a tenth in the raked area. In the raked area three-fourths were taken from soil; in the burned area over 99% from litter; and in the intact area nearly three-fourths from litter.

Remarks on Distribution. — Judged by the writer's collections, certain animals were usually associated with soil, others with litter, and a few varied in habitat with changes in environment. Earthworms and scarabaeid larvae were usually found in soil; millipeds varied with moisture and temperature conditions. In the raked area ants occurred in greater numbers in soil than in litter, but in the other two plots the opposite was true. Centipedes were usually found in litter, though they often went deeper. Scarabaeid adults, cockroaches, Machilis, mites, and spiders were regularly found in litter. At various seasons the following animals reached maximum numbers: spring, earthworms, in both litter and soil, and mites; summer, ants; autumn, spiders. Scarabaeid larvae were present more or less at all seasons except winter; adults occurred in summer and autumn. Cockroaches and millipeds were found in small numbers at all seasons. If results for various plots are compared (Table 2), the following animals were found to be most numerous in the area (32) that was left undisturbed: an earthworm (*Eisenia*), centipedes, millipeds, beetles, scarabaeid

larvae in litter, tenebreonid and elaterid larvae, cockroaches, *Machilis*, mites, and spiders. Dipterous larvae occurred in about equal numbers in the burned over and intact plots. No animals were most abundant in the two denuded plots, except scarabaeid larvae in soil as opposed to litter. One earthworm (*Diplocardia*) was rather evenly distributed through all the plots, but was slightly fewer in the burned over area.

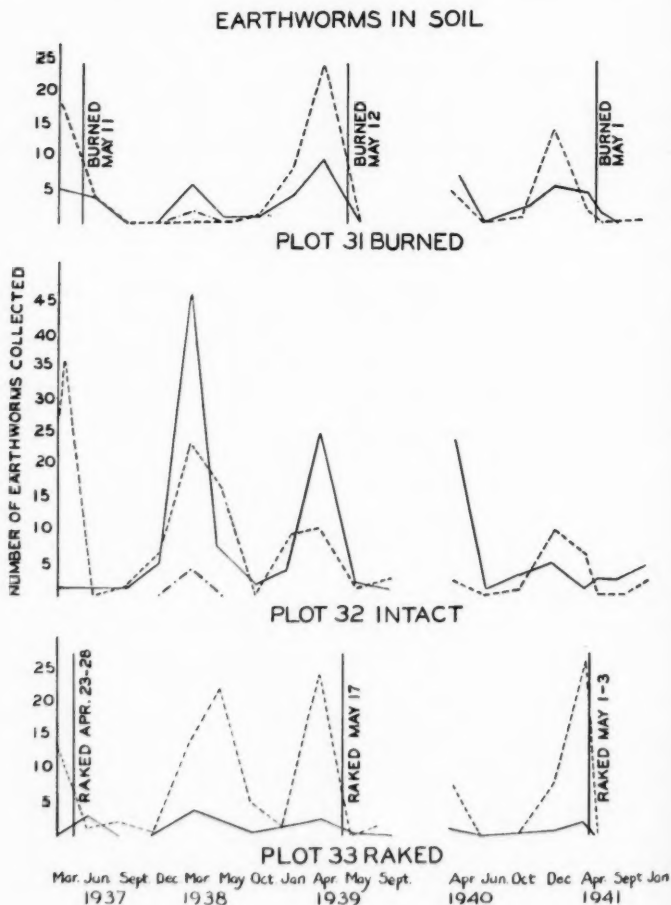


Fig. 1. Earthworms collected in the Duke Forest, 1937-1942.

TABLE 4.—Earthworms collected in the Duke Forest, 1937-1941. Figures show average number collected per day on nineteen days.

Species	Plot 31 Burned	Plot 32 Intact	Plot 33 Raked
<i>Eisenia carolinensis</i>	2.8	7.0	1.2
<i>Diplocardia michaelseni</i>	4.2	6.5	6.8
<i>Bimastus ducis</i>	0.1	0.2	0.0
Total	7.1	13.7	8.0

TABLE 5.—Centipedes and millipedes collected in the Duke Forest, 1937-1941. Figures show average number collected on 19 days.

	31-burned		32-intact		33-raked	
	Litter	Soil	Litter	Soil	Litter	Soil
Centipedes	14	9	46	22	7	5
Millipedes	3	1	13	2	1	14

TABLE 6.—Ants collected in the Duke Forest, 1937-1941.

	31-burned		32-intact		33-raked	
	Litter	Soil	Litter	Soil	Litter	Soil
Frequency	13	1	12	6	8	4
Total No.	326	2	770	316	50	139
Percent	99.4	0.6	70.9	29.1	26.5	73.5
Frequency	14		18		12	
Total No.	328		1086		189	
Percent	20.5		67.7		11.8	

List of Animals Collected from Soil and Litter

In the following list the plots are designated by number: 31, burned; 32, intact; and 33, raked. L. means litter and S. soil. Months and days are shown by Roman and Arabic numerals and the last figure shows the number collected or observed. For example, "31L, X4-'37:6" means that from sorted over litter on the burned plot, on October 4, 1937, six specimens were found.

Annelida

Specimens of earth worms from the Duke Forest were sent to the British Museum of Natural History, where they were identified by the late J. Stephenson and C. C. A. Monroe as belonging to the following nine species: *Allolobophora caliginosa* (Sav.) *trapezoides* (A. Dug.), **Bimastus ducis* Stephenson, *B. heimbürgeri* Smith, *B. zeteki* Smith & Gittins, **Diplocardia michaelseni* Eisen, **Eisenia carolinensis* Mich., *E. lönnbergi* (Mich.), *E. pearsei* Stephenson, and *Pheretima heterochaeta* Mich. Only three of these species (*) were found by the writer in the plots investigated. This statement is based on the assumption that all juveniles were the same as adults identified by the writer. They certainly belonged to the same genera and probably to the same species. The general distribution of the three species has already been discussed briefly. Seasonal distribution is shown in Fig. 3.

Arthropoda

CHELONETHIDA

Obisium sp. 32L, III 22-37:3 identified by Chandler.

ARACHNIDA
ACARINA

Mites were most often observed in the undisturbed plot (Table 2). Two specimens sent to Dr. H. E. Ewing were identified as species of the genera *Microtrombidium* and *Trombidium*.

ARANEIDA

Spiders were sent to A. M. Chickering for identification. He furnished the names in the following list. Many of the specimens collected were juvenile and therefore could not be identified to species.

CTENIGIDAE

Pachylomerides audouini (Lucas). Two trap-door spiders were taken: 31L, VI20-37:1; 31S, VII2-37:1.

DICTYNIDAE

Dictyna sp. 33L, IX28-41:1.

Scolothrips pallida (Marx). 31L, IV28-35:1; 32L, VI21-37:1.

SEGESTRIIDAE

Ariadna bicolor (Htz.). 31L, IX19-36:1; 32L, VI21-37:1; 32L, IX17-39:1.

GNAPHOSIDAE

Callilepis imbecilla (Keys.). 32L, VI21-37:1.

Drassodes neglectus (Keys.). 31L, V28-39:1; 32L, V28-39:1.

Drassodes sp. 31L, VI20-37:1.

Drassylus frigidus (Banks). 31L, IV6-41:1.

Drassylus sp. 31L, IX28-41:1; 32L, IX28-41:1.

Geodrassus sp. 31L, V29-38:1.

Gnaphosa sericata (L. Koch). 33L, V29-38:2.

Gnaphosa 2 sp. 31L, IX29-36:3; 31L, VI20-37:2; 31L, IX25-37:1; 32L, I3-39:1; 32L, V28-39:4; 32L, IX17-39:3; 32L, X6-40:2; 32L, VI8-41:1; 33L, VI20-37:1.

Lithophyllus sp. 31L, IX29-36:1; 31L, VI20-37:1; 31L, V28-39:1.

Rachodrassus sp. 32L, VI21-37:3.

Zelotes subterraneus (C. L. Koch). 32L, VI30-40:1; 32L, X6-40:3.

Zelotes sp. 32L, VI21-37:1.

THERIDIIDAE

Crustulina guttata (Wider). 33L, X6-40:1.

Dipoena sp. 33L, X6-40:1.

Latrodectus mactans (Fabr.). 32L, X6-40:1.

Lithyphantes sp. 32L, IX25-37:1.

Mysmena sp. 32L, VI21-37:1.

LINYPHIIDAE

Erigone sp. 32L, III27-37:1. Identified by Irving Fox.

Linyphia marginata C. Koch. 31L, X6-40:1; 32L, X2-38:1; 32L, IV-39:1.

MICRYPHANTIDAE

Ceraticelus alticeps Fox. 31L, IV28-35:2.

Ceraticelus sp. 31L, IX28-41:1.

Ceratinopsis interpres (Camb.). 31L, IV28-35:5; 31L, V28-39:1; 32L, III27-38:1.

Ceratinopsis sutoris Bishop & Crosby. 31L, X6-40:5.

Ceratinopsis sp., females. 31L, VI20-37:2; 32L, X6-40:4; 33L, X6-40:1.

Ceratinopsis sp. 31L, I13-35:1; 31L, IX19-36:2; 31L, VI20-37:2; 31L, IX28-

'41:2; 32L, X14-'34:2; 32L, VI21-'37:1; 32L, VI20-'40:1.

Microneta sp. 32L, X6-'40:1; 33L, IX17-'39:1.

Pelecopsis moestum (Banks). 31L, V6-'41:1.

ARGIOPIDAE

Aranea sp. 33L, V29-'38:1.

Mangora sp. 31L, IX28-'41:1.

THOMISIDAE

Philodromus sp. 32L, X6-'40:2.

Xysticus sp. 31L, VI20-'37:1; 31L, IV2-'39:1.

CLUBIONIDAE

Clubiona abbotii L. Koch. 32L, IX25-'37:1.

Clubiona sp. 31L, X6-'40:1.

Phrurotimpus alarius (Htz.). 31L, IV17-'35:1; 31L, IV2-'39:1; 31L, X6-'40:3; 32L, IX25-'37:1; 32L, V29-'38:1.

Phrurotimpus borealis (Emerton). 31L, VI20-'37:1; 32L, V29-'38:1.

Phrurotimpus sp. 31L, IV28-'35:1; 32L, IV2-'39:1; 32L, IX17-'39:1.

Scotinella pallida Banks. 32L, VI21-'37:1.

ANYPHAENIDAE

Anyphaena celer (Htz.). 31L, XII26-'37:1; 32L, IX17-'39:1.

Anyphaena pectorosa L. Koch. 31L, III7-'37:1.

Anyphaenella sp. 32L, X2-'38:1.

AGELENIDAE

Agelenopsis sp. 31L, IV3-'40:1; 31L, X6-'40:1; 31L, IV6-'41:1; 33L, IV6-'41:1.

HAHNIDAE

Hahnia cinerea Emerton. 31L, IV28-'35:1; 31L, VI20-'37:1; 32L, V28-'39:1.

Hahnia sp. 32L, V28-'39:1.

Neantistea agilis (Keyes). 31L, IV28-'35:1; 32L, IX17-'39:1; 33L, X2-'38:1.

PISAURIDAE

Dolomedes sp. 31L, II3-'35:1.

LYCOSIDAE

Lycosa avara (Keys.). 31L, X6-'40:1; 32L, X14-'34:2; 32L, X2-'38:2; 33L, X2-'38:1; 33L, X6-'40:1.

Lycosa frondicola Emerton. 32L, VI21-'37:1.

Lycosa sp. 31L, II3-'35:1; 31L, IX17-'39:1.

Pardosa 2 sp. 31L, IX19-'36:4; 31L, III7-'37:2; 31L, IX25-'37:2; 31L, III27-'38:1; 31L, V29-'38:1; 31L, X2-'38:5; 31L, IV2-'39:1; 31L, V28-'39:1; 31L, IX17-'39:1; 31L, X6-'40:7; 32L, IV6-'41:2; 32L, III7-'37:1; 32L, IX25-'37:4; 32L, III27-'38:1; 32L, X2-'38:4; 32L, IX17-'39:1; 32L, IV3-'40:1; 32L, X6-'40:3; 32L, IV6-'41:1; 32L, IX28-'41:2; 33L, III7-'37:1; 33L, IX25-'37:1; 33L, X2-'38:1; 33L, V28-'39:1; 33L, IX17-'39:1; 33L, XII23-'40:1.

Schizovosa crassipes (Walck.). 31L, IX19-'36:3; 32L, V28-'39:1.

Schizocosa saltatrix Htz. 31L, V29-'38:4; 31L, VI30-'40:1; 32L, VI21-'37:1; 32L, III27-'38:2; 32L, V29-'38:4; 31L, VI30-'40:1; 32L, VI21-'37:1; 32L, III27-'38:2; 32L, V29-'38:1; 33L, VI30-'40:2.

Schizocosa sp. 31L, IV28-'35:1.

Trabaca aurantiaca (Emerton). 32L, IV2-'39:1.

SALTICIDAE

Habronattus sp. 31L, IV6-'41:1; 32L, IX28-'41:1.

Icius sexmaculatus Banks. 32L, IX25-'37:2; 32L, IX17-'39:1; 33L, X6-'40:1.

Maevia vittata (Htz.). 32L, V28-'39:1.

Metaphidippus sp. 31L, IV28-'35:2.

Neon nellii Peckham. 31L, IX19-'36:1; 32L, V29-'38:1.

Paraphidippus marginatus (Walck.). 31L, V2-'38:1.

Talavera minuta Banks. 32L, VI21-'37:2.

Thiodina puerpera (Htz.). 32L, V29-'38:1.

New genus? 32L, X6-'40:1.

PHALANGIDA

Leiolum calcar Wood. 33L, XII26-'37:1.

DIPLOPODA

Millipedes were identified by Dr. Nelle Bevel Causey. *Cleidogona caesioannulata* (Wood). 32L, X6-'40:1; 32L, XII23-'40:1; 32L, IX28-'41:1.

Fontariidae juv. 33L, VI20-'37:1; 33L, IV6-'41:2; 33S, III7-'37:1; 33S, XII26-'37:12; 31L, III7-'37:1; 32L, V29-'38:1.

Spirobolus marginatus Say. 31S, VI20-'37:1.

By using Berlese funnels Dr. J. H. Starling has found six species of diplopods in the Duke Forest, whereas the writer observed only four. Of course the methods used by the writer would not demonstrate the presence of such minute animals as polyxenids, though they are known to be abundant in many parts of the forest.

CHILOPODA

Centipedes were identified by Dr. Nelle Bevel Causey.

Cryptops hyalinus, Say. 31L, IX28-'41:1.

Garibius georgiae Chamberlin. L33, III7-'37:1; 33S, X6-'40:1.

Geophilus varians McNeill. 31L, III7-'37:1; 31S, V29-'37:1; 33L, III27-'37:1; 32L, XII 26-'37:1; 32L, III 27-'38:1; 32S, I7-'42:1.

Gnathomerium umbraticum (McNeill). 31L, VI 20-'37:1; 31L, V29-'38:1; 32L, VI8-'41:1; 33L, XII26-'37:2.

Linolenia bidens (Wood). 31L, I3-'39:1.

Lithobius atkinsoni Bollman. 32L, III22-'37:1; 32L, III2-'38:2.

Nampabius carolinensis Chamberlin. 32L, VI21-'37:3.

Otocryptops sexspinosus (Say). 31L, VI20-'37:1; 31L, XII23-'40:1; 31L, IV6-'41:1; 32L, III7-'37:1; 32L, III22-'37:1; 32L, VI21-'37:2; 32L, III29-'38:1; 32L, VI30-'40:1; 32L, VIII28-'41:2; 32S, III27-'38:4; 32S, X6-'40:1; 32S, IX28-'40:1; 32S, I7-'42:2; 33L, V29-'38:1; 33L, XII23-'40:1.

Pachymerium ferrugineum (C. L. Koch). 32L, XII-'40:1.

Paitobius zinus (Chamberlin). 31L, VI20-'37:1; 32L, VI21-'37:3.

Sigibis starlingi Causey. 33L, IX25-'37:1; 32L, III27-'38:1.

Theatops posticus (Say). 31L, XII23-'40:2; 32L, V29-'38:2; 32L, IX28-'41:1; 32S, IX25-'37:1; 32S, III27-'38:1; 32S, X6-'40:1; 33L, IV6-'41:1.

Dr. Starling with Berlese funnels collected 28 species of centipedes in the litter and soil of the Duke Forest, and the writer observed twelve species.

Dr. Starling also collected four species of symphylans and six species of pauropods, but the writer observed none.

INSECTA

THYSANURA

Machilis variabilis Say. 31L, VI30-'40:2; 32L, VI20-'37:1; 32L, X2-'38:1; 32L, IV2-'39:1; 32L, VI3-'40:2; 32L, VI8-'41:3; 33L, IX25-'37:1; 33L, IX17-'39:1; 33L, VI30-'40:1; 33L, X6-'40:1; 33L, VI8-'41:1. This insect is common in the Duke Forest, where it runs about over litter, logs, and the bases of trees (Ramsey 1941).

APTERA

Japygidae

Japyx subterraneus Packard. 33S, IV3-'40:1. Identified by H. E. Ewing.

COLLEMBOLA

Collembolans were identified by Dr. Harlo B. Mills.
Isotoma viridis Bourl. 31L, XII26-'37:10; 32L, III27-'38:8.
Lepidocyrtus unifasciatus James. 32L, VI30-'40:5.

Onychiurus subtenius Folsom. 32L,V29-'42:2.

Orchesella sp. 32L,V29-'38:2.

Pseudosinella violenta Folsom. 31L,VI20-'37:50; 32L,V29-'38:3.

Tomocerus flavescens (Tullberg). 32L,VI21-'37:100; 32L,XII26-'37:10; 32L,III27-'38:22; 32L,IV2-'39:25; 32L,IX17-'39:8; 32L,VI30-'40:10; 32L,IX28-'41:4. This species was found only in the litter of the intact plot (.32) and was at times abundant.

Tomocerus sp. 32L,V29-'38:3.

ORTHOPTERA

Mr. A. B. Gurney identified orthopterans.

Tettigoniidae

Atlanticus pachymerus (Burm.). 31L,I3-'39:1.

Gryllidae

Cycloptilum bidens Heb. 31L,IX17-'39:1; 32L,VI21-'42:1.

Gryllus assimilis (F.). 31L,X6-'40:1; 32L,IX17-'39:1; 32L,IX28-'41:1.

Nemobius fasciatus tinnulus Fulton. 31L,X2-'38:2; 31L,X6-'40:3.

Blattidae

Cariblatta lutea lutea (S. & Z.). 31L,X6-'40:2; 32L,IV2-'39:1; 32L,VI18-'41:1; 32L,X6-'40:6.

Ischnoptera deropeltiformis Brunn. 31L,X6-'40:1; 32L,IX17-'39:3; 32L,X2-'38:3; 32L,IX28-'41:2.

Parcoblatta fulvescens (S. & Z.). 32L,VI30-'40:1.

Parcoblatta sp., nymphs. 31L,III7-'37:1; 31L,V29-'38:1; 31L,I3-'39:1; 31L,S6-'40:7; 31S,II3-'35:1; 32L,I3-'39:1; 32L,IV2-'39:1; 32L,V28-'39:2; 32L,IX17-'39:4; 32L,X6-'40:1; 32L,IV6-'41:1; 32L,VI18-'41:2; 32L,IX25-'37:1; 33L,I3-'39:1; 33L,IV2-'39:1; 33L,VI30-'40:1.

Parcoblatta or *Ischnoptera*; egg cases. 31L,X6-'40:1; 31L,IV6-'41:1; 32L,I3-'39:1; 32L,V28-'39:1; 32L,IX17-'39:2; 32L,X6-'40:1; 33L,V28-'39:1.

ISOPTERA

Termites were identified by Dr. T. E. Snyder. The writer supposed that only one species of termite occurred in the Duke Forest, so did not save specimens at all times when they were found. Total collections were as follows: 31L, V29-'38:65; 31L,X2-'38:10; 31L,X6-'40:5; 31S,IX19-'36:50; 32L,VI21-'37:6; 32L,V29-'38:30; 32S,IX17-'39:10; 32S,IV6-'41:5; 33L,IX25-'37:2; 33S,XII26-'37:30; 33S,V28-'39:30. Three lots of these that were sent to Dr. Snyder were:

Reticulitermes flavipes Kollar. 31L,X6-'40:5.

Reticulitermes virginicus Banks. 31S,IX19-'36:50; 33S,V28-'39:30.

NEUROPTERA

Sialidae

Nigronia sp., or a closely related genus. A. B. Gurney who identified a single specimen that was found, believed that it was probably the pupa of an aquatic larva that had crawled from some nearby body of water. 31S,V28-'39:1.

HETEROPTERA

Bugs were identified by H. G. Barber.

Lygaeidae

Oedancala dorsalis (Say). 31L,IV2-'39:1.

Pentatomidae

Brochymena carolinensis (Westw.). 33L,I3-'39:1.

Solubea pugnax (F.). 31L,X6-'40:1.

HOMOPTERA

Homopterans were identified by P. W. Oman.

Cicadidae

Dicoroprocta viridifasciata (Walk.). An empty skin taken on the base of a tree probably belonged to this species. 32, IX28-'41:1.

Fulgoridae

Epiptera sp.; nymphs. 31L, II3-'35:1; 31S, II3-'35:2.

COLEOPTERA

Carabidae

Carabids were determined by J. M. Valentine.

Cyclotrachelus rotundatus Lec. 31S, IV2-'39:1; 32S, IX28-'41:1; 33L, X2-'38:1; 32L, IV6-'41:1.

Dicaelus dilatatus Say. 31S, X2-'38:1; 31S, IV2-'39:1.

Evarthrus sp. 31S, IV28-'39:1; 32L, III27-'38:1; 32S, XII26-'37:1; 32S, III27-'38:1.

Notophilus novemstriatus Lec. 31L, X6-'40:1; 31S, IV2-'39:1; 32L, III27-'38:1; 33L, V28-'39:2; 33L, IV6-'41:1.

Tachys (Microtachys) laevis Say. 31L, X2-'38:1; 32L, III7-'37:2; 32L, II22-'37:2; 32L, III27-'38:3; 32L, IV2-'39:3.

Staphylinidae

Tayporinae, according to W. H. Anderson. 32L, III22-'37:1. Other scarabaeids were collected, but not identified.

Pselaphidae

Small "ant-guest" beetles were often observed in the litter of the Duke Forest. Miss Caroline E. Powell has identified *Tmesiphorus costalis* Lec. and *Tychus minor* Lec. as common, representative species there. The writer's records of what he took to be pselaphids were as follows:

31L, X6-'40:1; 32L, III1L-'37:1; 32L, VI21-'37:20; 32L, XII26-'37:4; 32L, V29-'38:50; 32L, X2-'38:2; 32L, I3-'39:1; 32L, IV2-'39:10; 32L, V28-'39:2; 32L, IX28-'41:2.

Nitidulidae

Steliodota geminata (Say). 33L, V4-'28:1.

Scydmenidae

Connophron anale (Lec.). 32L, III27-'38:2. Identified by W. S. Fisher.

Scaphidiidae

Shining fungus-beetles were identified by H. S. Barber.

Baeocera sp. 32L, XII26-'37:1; 32L, III27-'38:5.

Lampyridae

Photinus castus Lec. 32L, VI30-'40:1. Identified by H. S. Barber.

Elateridae

Elaterid larvae were quite common. They were identified by W. H. Anderson.

Limonius sp. 31S, VI20-'37:1.

Melanotus sp. 31L, IV2-'39:2; 31S, IX17-'39:1; 31S, X6-'40:1; 32L, X2-'38:1; 32L, I3-'39:1; 32L, IX17-'39:1; 32L, IV6-'41:2; 32S, III27-'38:1; 32S, IV2-'39:2; 32S, V28-'39:2; 32S, VI30-'40:1; 32S, X6-'40:2; 33S, III7-'37:1.

Sericus sp.? 32L, V29-'38:1.

Tenebrionidae

Darkling beetle larvae were identified by W. H. Anderson.

Helops sp. 31S, VI20-'37:1; 32L, IX28-'41:1; 33L, III30-'39:1; 33S, III27-'38:1; 33S, IV6-'41:1.

Ipthimus sp.? 31L, II3-'35:3.

Mercanthera contracta (Beauv.) 32L, III22-'37:1; 32L, IV2-'39:1; 32S, V28-'39:1; 33L, IV2-'39:1.

Genus unknown. 32S, III22-'37:1.

Scarabaeidae

White grubs and May-beetles were identified by W. H. Anderson and E. A. Chapin; number for imagoes are in italics.

Anomala sp.? 32S,V29-'38:1; 31S,IV2-'39:1.
Diplotaxis liberta (Germar). 31L,IX17-'39:1; 32L,IX17-'39:3; 33S,IV3-'40:1; 31L,IV3-'40:1; 31L,X6-'40:1; 31S,X6-'40:1; 32L,IV6-'41:1; 33L,IV6-'41:1; 31L,IV6-'41:2; 31S,V18-'41:2; 31L,IX28-'41:1.

Diplotaxis sp. 31S,V120-'37:7, 1 pupa; 31S,IV2-'39:1; 31S,V28-'39:3; 31S,X6-'40:1; 33S,V120-'37:7; 33S,III27-'38:1; 33S,III30-'39:1; 33S,V28-'39:2; 33S,X6-'40:1; 33S,IX8-'41:1. All specimens were found in burned or raked plots.

Macrodactylus subspinosus ? (F). 31L,I3-'39:1; 33L,V28-'39:1 pupa.

Phyllophaga profunda (Blanch). 32S,IX28-'41:10.

Phyllophaga quercus (Knoch). 31L,IV3-'40:1; 31S,IV2-'39:1; 31S,V29-'38:1; 31S,X6-'40:3; 32S,IV3-'40:1; 33S,V120-'37:2; 33S,III27-'38:1.

Phyllophaga fraterna Harris. 32S,I7-'41:1.

Canthon viridis Palis. 32L,IV2-'39:1.

Ataenius sp. 32L,IV2-'39:1.

Chrysomelidae

Leaf-beetles were identified by H. S. Barber.

Metachroma sp. 33L,VI30-'40:1.

Paria sp. 32L,III22-'37:23.

Coccinellidae

Mulsantia picta (Rand.). 31L,I3-'39:2.

Curculionidae

Apion decoloratum Smith was identified by L. L. Buchanan. 32L,V29-'38:30; 32L,IX28-'41:1.

LEPIDOPTERA

Tortricidae

A caterpillar was identified by Carl Heinrich as:

Archips sp. 31L,X6-'40:1.

HYMENOPTERA

Pamphiliidae

A larva was identified by R. A. Cushman as:

Acantholyda sp.? 33L,V29-'38:1.

Diprionidae

A sawfly cocoon was identified by R. A. Cushman as:

Neodiprion sp.? 32L,IV2-'39:1.

Calliceratidae

C. F. W. Huesebeck identified a single specimen as:

Lagynodes sp. 32L,V29-'38:1.

Mutillidae

K. V. Krombein identified a single imago as:

Timulla ornatipennis (Brad.) 31L,V120-'37:1.

Formicidae

Ants were mostly identified by Caroline E. Powell, and a few by M. R. Smith.

Aphaenogaster treatae Forel. 32L,IX17-'39:8.

Camponotus mississippiensis Smith. 31L,XII26-'37:1; 31L,IV6-'41:5; 31L,IX28-'41:3; 32L,IX25-'37:40; 32S,III1-'37:1; 33L,I3-'39:1; 33L,V28-'39:5.

Crematogaster laeviuscula Mayr. 32L,IV2-'39:2; 32S,IV2-'39:135.

Crematogaster lineolata Say. 31L,IV6-'41:100; 32L,V29-'38:40; 32L,VI30-'40:31; 32L,IX17-'39:36; 32S,V28-'39:10.

Dorymyrmex pyramicus flavus McCook. 33S,V28-'39:20.

Formica pallide fulva Latr. 32S, IX28-'41:8.

Lasius umbratus mixtus Nyl. 32L, V29-'38:30; 32L, VI30-'40:20; 32S, V28-'39:30; 33S, IX25-'37:150.

Leptothorax curvispinosus Mayr. 31L, IX25-'37:5; 31L, V29-'38:20; 31L, X2-'38:4; 31L, IV2-'39:2; 31L, IX17-'39:1; 31L, IV3-'40:1; 31L, VI3-'40:3; 31L, X6-'40:10; 31L, IV6-'41:1; 31L, VI8-'41:1; 31L, IX28-'41:3; 31S, IV18-'41:2; 32L, III22-'37:15; 32L, IX25-'37:60; 32L, III27-'38:20; 32L, V29-'38:15; 32L, X2-'38:1; 32L, V28-'39:3; 32L, VI30-'39:3; 32L, X6-'40:3; 32L, IV6-'41:1 ♀; 32S, III22-'37:1; 32S, V28-'39:75; 33L, IX25-'37:1; 33L, V29-'38:1; 33L, V28-'39:6; 33L, IX17-'39:2; 33L, VI30-'40:8; 33S, X6-'40:2.

Monomorium pharaonis L. 31L, IX19-'36:3.

Prenolepis imparis testacea Emery. 32S, V29-'38:5; 33S, X6-'40:2.

Prenolepis longicornis Latr. 31L, IV2-'39:1; 31L, V28-'39:15; 32L, III22-'37:5; 32L, V28-'39:3; 33L, IX7-'37:1; 33L, VI30-'40:3.

Solenopsis molesta Say. 31L, VI20-'37:30; 32L, III7-'37:1.

Tapinoma sessile (Say). 32L, IX17-'39:7.

DIPTERA

Tipulidae

Larval tipulids were identified by C. T. Greene. 31L, IV2-'39:2; 33L, VI8-'41:1.

Culicidae

Mosquitoes were identified by Alan Stone.

Anopheles punctipennis (Say). 31 air, IV28-'35:1.

Psorophora ferox (Humb.) 31 air, IX25-'37:6; 32 air, IX25-'37:6; 32 air, IX17-'39:5.

Fungivoridae

Lycoria sp., identified by Alan Stone. 32L&air, VI30-'40:5.

Itionididae

An immature gall gnat was identified by C. T. Greene. 32L, VI30-'40:1.

Simuliidae

Black-flies were identified by Alan Stone.

Prosimulium hirtipes (Zett.). 31 air, III7-'31:15.

Tabanidae

Tabanid larvae were identified by C. T. Green.

Tabanus sp. 31S, IV28-'35:2; 31S, III7-'37:1; 31S, X2-'38:1; 31S, I3-'38:1; 31S, IV2-'39:1; 32S, X2-'38:1; 32S, I3-'38:3; 32S, IV2-'39:2; 32S, XII23-'40:1; 32S, I7-'42:1; 33S, III27-'38:1; 33S, X2-'38:1; 33S, I3-'38:1; 33S, IV6-'41:1.

Bombyliidae

Bee-flies were identified by C. T. Greene.

Anthrox sp. 31L, IV3-'40:1.

Sparnopolius sp.? 31L, III7-'37:1; 31L, X6-'40:1; 32S, IX28-'41:1.

Therevidae

Stiletto-fly larvae were identified by C. T. Greene.

Philocephala sp.? 32L, III27-'38:3.

Mydidae

Mydas-fly larvae and a pupa (*) were identified by C. T. Greene.

Mydas sp. 31S, VI20-'37:1; 32L, IX28-'41:1; 33S, VI20-'37:1; 33S, V28-'39:1*; 33S, IV6-'41:1; 33S, I7-'42:1.

Syrphidae

Syrphids were identified by C. T. Greene.

Metasyrphus sp. 33L, IV3-'40:1 cocoon.

Syrphus sp. 32 air, IV3-'40:1.

Mollusca**GASTROPODA**

Zonitoides arboreus Say. 32L,IV2-'39:1 juv.

Chordata**AMPHIBIA**

Plethodon cinereus (Green). 32L,III27-'38:2.

Plethodon glutinosus Green. 33S,XII23-'40:2.

REPTILIA

A worm snake was identified by I. E. Gray.

Carphophis amoena amoena (Say). 32L,IV2-'39:1.

MAMMALIA**LAGOMORPHA**

Sylvilagus floridanus mallarus (Allen). The occurrence of rabbit feces is shown in Table 2. Such remains were most often encountered (8) on the intact plot; half as many (4) were found on the raked area; and fewest (2) on the burned area.

Discussion

Soil animals live in a habitat that has greater stability than those in which epigeal types exist. They are in less danger from extreme changes in temperature, excessive radiation, and desiccation. They are dependent directly or indirectly for food on the plants above the surface; they are generally able to live in low concentrations of oxygen and therefore often have slow rates of metabolism; they usually have little toleration for high temperatures and light intensities. Organic remains in soil usually make it more favorable for animals, by furnishing food and by making soil more porous and penetrable. Animals in soil make it more favorable for plant growth, more porous and better aerated. The importance of bacteria and other fungi in soil formation is of course well known (Waksman 1932). Taylor (1928) designates microfauna, insects, reptiles, birds, and mammals as soil makers. The burrows of rodents (Taylor 1928) and ants (Branner 1912) are especially significant. Near such borrows there are mineral salts (Ca, Mg; CO₃, NO₃, etc.) (Greene & Reynard 1932). A layer of forest litter over soil serves as a loose organic blanket that increases environmental stability for soil animals. Rains that may drive all air out of soil and litter then is especially valuable as a shelter.

The studies described in this paper are concerned with the effects of the partial removal of litter by burning and total removal by raking on macroscopic soil animals. Either procedure makes environmental conditions in soil more variable. Burning over makes soil more alkaline and some animals, such as certain earthworms (Table 2) that are sensitive to changes in ionization (Arrhenius 1921, Allee, Torvik, Lahr, & Hollister 1930), became fewer. Other animals probably decrease in numbers because there is less water and because temperature variations are extreme. In soil from which litter has been completely removed particles tend to become fine and packed together into crusts. After rains water runs off quickly and carries soluble salts with it. So litterless soils tend to become barren; unproductive of plants and with few or no soil animals. Table 3 shows that about two-fifths of the soil animals collected by the writer in the Duke Forest were in the intact plot, and a fifth in each of

the burned and raked plots. In other words, three times as many animals were present in the intact plot as in either of the others. The first to disappear after denudation were minute animals (mites, collembolans). Those that persisted under most adverse conditions were small earthworms (*Diplocardia*, which probably retreated under tree bases during dry periods), certain beetle larvae (*scarabaeids*), and some arthropods that ran in and over litter (cockroaches, certain spiders and ants). Millipedes lived in litter in the intact plot, descended into the soil and persisted on the burned area, but almost deserted the raked area (Table 2).

Most writers on soil organisms give estimates of number present per acre. As Trägårdh (1933) has pointed out numbers obtained from soil samples vary enormously with slight differences in collecting methods, soil conditions, seasons, etc. Shindo (1929) found more earthworms and nematodes in grassland than in forest. Waksman (1932) states that soil bacteria are generally most abundant in forests. He estimates that an acre may contain 16.2 lbs. of soil animals, a half of which would be earthworms. The writer's studies were made on poor forest soils and his methods discovered only common macroscopic animals, but a few estimates may be of interest. For example, on June 20, 1937 the following numbers of animals per acre were indicated (Table 3):

Plot 31 — litter:	291,610;	soil:	26,620;	total:	318,230
Plot 32 — litter:	792,550;	soil:	1,210;	total:	793,760
Plot 33 — litter:	35,090;	soil:	100,430;	total:	135,520

On September 25, 1937, the numbers per acre were:

Plot 31 — litter:	10,890;	soil:	1,210;	total:	12,100
Plot 32 — litter:	150,040;	soil:	8,470;	total:	158,510
Plot 33 — litter:	31,460;	soil:	186,340;	total:	217,800

Probably such estimates are all very far from the true number of macroscopic animals present, a single collembolan in a sample would change a total 1210, but they give a general idea of populations.

Summary

1. For five years macroscopic litter and soil animals were collected every three months from three plots in a pine stand in the Duke Forest. One plot was left intact; one was burned over; and the other was cleaned completely of litter every two years.
2. Collections covered 35 sq. ft. of litter and soil to a depth of three inches.
3. From the three plots the following numbers of animals were collected:
Intact — litter: 1675; soil: 603; total: 2278; 59%.
Burned over — litter: 659; soil: 208; total: 867; 22.5%.
Raked — litter: 149; soil: 569; total: 718; 18.5%.
4. Removal of litter changes soil as a habitat for animals and many of them die or decrease in numbers. Burning over apparently is not as detrimental as complete removal of forest litter.

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Notes on the Turbellarian Fauna of Rochester (N. Y.)
with Special Reference to the Anatomy of
Macrostomum ontarioense n. sp.*

Frederick Ferdinand Ferguson

Monroe County, New York, is of especial interest to students of Turbellarian fauna because it is one of the few places in our country where comparisons may be made of the fauna at present with that existing in 1884 and 1911 when Silliman and Graff, respectively, described their findings. Of interest also is the Genesee River Falls in this area since it is the habitat of that most striking of American species of Rhabdocoelida, *Mesostoma ehrenbergii* var. *wardii* Ruebush, whose chromosomes ($N=4$, $2N=8$, length up to 32μ) and large translucent body (7 mm.) make it valuable as an experimental form. The many excellent aquatic habitats abounding in and near Rochester present a profitable field from which to obtain information on these organisms. Our present knowledge upon the Turbellaria of this region shows that species of the following genera have been studied: *Catenula*, *Stenostomum*, *Dalyellia*, *Microdalyellia*, *Castrella*, *Mesostoma*, *Phaenocora*, *Microstomum*, *Prorhynchus*, *Jensenia*, *Olisthanella*, *Strongylostoma*, *Rhynchomesostoma*, *Typhloplana*, *Castrada*, *Gyratrix*, *Polycystis*, and *Macrostomum*. The following is a description of a new species of *Macrostomum* (Rhabdocoelida).

Macrostomum ontarioense n. sp.

Ecology.—*Macrostomum ontarioense* was first taken from the rough open shore line waters of Grand View Beach, Lake Ontario in early September, 1941. It was associated with an unusually large number of Protozoa and Crustacea mixed with algae. Altitude, about 247 feet. Geology, glacial.

Description.—Body colorless except for brownish enteron, dorsoventrally compressed (Fig. 1), extremities rounded, broadest at midbody level. Length ca. 560μ , width 140μ . Epidermis of flat pentagonal cells (ca. 5μ thick) with an overall even coat of cilia. Sensory spines disposed anteriorly (ca. 8μ), posteriorly lacking. Sensory hair tufts overall, posteriorly in groups of 2 and 3 (ca. 28μ), laterally sparse. Rhabdoids consist of abundant, uniformly dispersed adhesive rods (*Rhabdites*) in groups of 7-8 on the dorsum, of strongly developed anterior streamers of adenal filaments (*Rhabditen-Strassen*) dorsal and ventral to the brain and of ovoidal rods (*Stäbchen*) ventro-radially dispersed at the female gonopore. Brain of semi-lunar contour (ca. 20μ thick in mid-line), commissure not discrete. Eyes paired (Fig. 2) and black (ca.

* A research award of the A.A.A.S. through the Virginia Academy of Science has materially aided in this work.

12 μ long) exactly posterior to brain, closer to each other than to sides of body, pigment granules quite small and not of uniform size. Mouth limited by longitudinal ciliated lips, located antero-ventrally in mid-line (ca. 120 μ long), abundantly supplied with adenal (*Rhammiten*) glands. *Pharynx simplex* well developed, possessed of latero-posteriorly directed streamers of granule and rhabdoidal gland cells. Enteron colorific, sac-like, longitudinally extending dorsal to female genital atrium, with ciliated endodermal epithelium. Excretory system of paired lateral protonephridia apparently separate, external openings not observed. Testes obovate, smooth walled, latero-ventrally disposed. Vesicula seminalis of all specimens studied considerably distended (ca. 35 μ in diameter) with sperm cells, walls quite thin. Portal between sperm and granule sacs prominent. Vesicula granulorum relatively small with a central ciliated crypt, distally supplied with numerous rosettes of small graniferous cells extending far into genital canal of penis stilette. Penis stilette a sharply terminated conical tube with two distinct right angle flexures in different planes somewhat simulating a coiling, base crenated (ca. 13 μ in diameter), length ca. 32 μ , external opening terminal with outlet on left side, shows all but last flexure in a dorsal plane, point of stilette is most ventral part of last flexure and is slightly recurved. Ciliated male gonopore very close to posterior end of body. Ovaries paired and lateral, highly granular and indented, rest of female sex apparatus regular. Eggs spherical, grayish-black in female genital atrium (ca. 100 μ in diameter). Sperm cells undifferentiated threads (ca. 20 μ long) except for a central chain of spheroidal granules (usually 3 to 4), *Nebengeisseln* lacking.

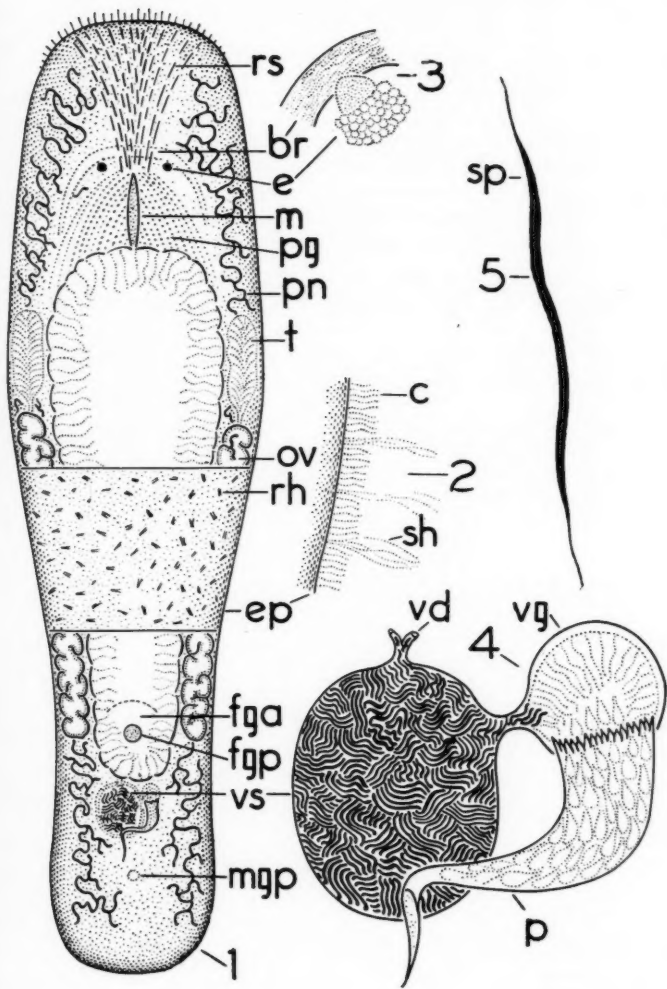
Taxonomic disposition.—Reference to the monograph on the genus *Macrostomum* (Ferguson, 1939-1940) shows that *M. ontarioense* is more closely related to *M. viride*, *M. collistylum* and *M. lineare* than to other species.

This species is compared to *M. viride* van Beneden because it has an S-shaped penis stilette (See van Beneden, 1870, p. 11). The stilette of the Rochester form has an S-shaped copulatory organ only in the sense that it is doubly flexed. In several other characters these two organisms differ markedly.

M. collistylum Ferguson and *M. lineare* Uljanin have stilettes which are quite distinctly coiled by flexures involving arcs of from 315° to a complete

LEGEND TO TEXT FIGURES

br—brain	pg—pharyngeal glands
c—cilia	pn—protonephridium
ce—ciliated enteron	rh—rhabdite
e—eye	rs— <i>Rhabditen-Strassen</i>
ep—epidermis	s—sperm cell
fga—female genital atrium	sh—sensory hairs
fgp—female genital pore	sp—sensory spines
m—mouth	t—testis
mcp—male genital pore	vd—vas deferens
ov—ovary	vg—vesicula granulorum
p—penis stilette	vs—vesicula seminalis



Figs. 1-5. *Macrostomum ontarioense*, n. sp. 1. Gross anatomy showing most of body in dorsal optical section. $\times 275$.—2. Detail of epidermal cilia and sensory hair tufts. $\times 750$.—3. Detail of eye. $\times 750$.—4. Detail of male sex apparatus. $\times 1500$.—5. Detail of mature sperm cell. $\times 3750$.

circle (See Ferguson, 1939, p. 189, Fig. and Uljanin, 1870, p. 9, Fig. 1.). Viewed in dorsal optical section under oil immersion it may be seen that the penis stilette of the New York flatworm begins its curving very near the wide crenated base (Fig. 4), bends to the left as the tube narrows abruptly, dips ventrally at the next turn and finally slightly recurves in its sharpened terminus; thus most of the proximal tube may be viewed in a dorsal plane while the narrowed distal region is seen in a ventral plane of focus. In establishing this form as a new species, it is of interest to note that it belongs to a small group of species whose sperm cells possess rows of chromatin granules as discussed by Phillips (1936). Co-type material will be deposited in the U.S. National Museum.

Differential Diagnosis.—*Macrostomum ontarioense*. Body colorless, extremities rounded, length 0.5 mm. *Rhabdites*, *Stäbchen* and *Rhammiten* abundant. Epidermal cilia, sensory spines and hair tufts present. Brain of semi-lunar contour, without marked commissure. Vesicula semianalis thin walled extensive sac, vesicula granulorum small with central ciliated crypt and distal rosette of granuliferous cells. Penis stilette an extended, sharply pointed funnel with two right angle bends, producing a peculiarly twisted tube whose parts do not lie in same plane, length 32μ , external opening on left side of pointed terminus. Male gonopore very near posterior tip of body. Sperm cells elongate threads with a row of chromatic granules but without *Nebengeisseln*, length 20μ .

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Revision of the Western North American Species of *Aster* Centering About *Aster foliaceus* Lindl.*

Arthur Cronquist

This study is intended to include the western North American forms of *Aster* proper that are not entirely glabrous and have eglandular involucre, exclusive of the rigid forms centering about *Aster commutatus* T. & G. and *Aster radulinus* Gray, of such chartaceous-involucrate forms as *Aster alpinus* L. and *Aster meritus* A. Nels., and of such primarily eastern forms as *Aster longifolius* Lam. and *Aster Lindleyanus* T. & G. that reach the edges of our range but in general do not form an integral part of our western *Aster* flora. By western North America is meant the area from the Rocky Mountains, exclusive of the Black Hills, to the Pacific Ocean, north of Mexico. The species which occur east of our range as well as within it are treated only with respect to western North America. As so delimited, the forms treated in this paper, with the possible exceptions of *Aster coerulescens* and *Aster Gretaia*, constitute a wholly natural group.

The history of taxonomic treatments of North American *Aster* is extremely varied. Asa Gray (1884) recognized 14 species and 13 additional varieties in the group here treated. Rydberg (1917), who treated most of these forms except the ones exclusively Californian, recognized 49 species and no varieties. In the present treatment it is proposed to maintain 8 species, 3 subspecies, and 13 varieties.

The first important treatment of the group with which we are concerned was that of Torrey and Gray (1841). They recorded 12 species and 3 varieties in this group, including every species recognized in this paper except two endemics. Because of the paucity of material available at that time, affinities were very difficult to ascertain, so that the names in which we are interested are scattered through some 50 pages of text. Even at that early date most of our recognizable kinds of *Asters* had been discovered, although multiplication of names continued for over three-quarters of a century.

The next important treatment of the group was that of Asa Gray (1884). In his truly monumental work Gray treated every form recognized in the present revision, excepting the two aforesaid endemics. Even he listed as species or varieties some 13 names which are here reduced to synonymy. Considering the inadequate material available to him, one must admit that Gray did a truly remarkable job on our western *Asters*. It is no discredit to him that subsequent collections have revealed a need for further reductions.

The 30 years immediately following the publication of the Synoptical Flora was a period of unprecedented activity in naming new species. E. L.

* Condensed from a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at the Utah State Agricultural College in May, 1940.

Greene and P. A. Rydberg, with a much narrower species-concept than had previously prevailed, contributed most of the names of this period. Various manuals covering parts of the area of the present treatment appeared meanwhile. Among them are those of Piper (1906, Washington), Coulter & Nelson (1909, Rocky Mountains), Rydberg (1917, Rocky Mountains), Jepson (1925, California), and Tidestrom (1925, Utah and Nevada). Extremely diverse treatments were accorded the group in these works, and none of them included all the forms here considered.

Max Onno, a worker at the University of Vienna, published in 1932 a treatment of *Aster alpinus* L. and related forms, the section *Alpigeni* of Nees. He has apparently done very little field study outside of Europe, as the following quotation from his paper indicates: "Bei *A. alpinus*, der einzigen Art, von der ich lebendes Material gesehen habe . . ." The American forms are treated very artificially as well as superficially, inasmuch as *Xylorhiza* is included in the section *Alpigeni* along with *A. foliaceus*, while forms very closely related to *A. foliaceus*, as *A. Douglasii*, are excluded as belonging to the section *Euaster*. Another quotation will perhaps indicate the extent to which his work can be used for our forms: "Bei den Amerikanischen Arten, besonders *Xylorhiza*, musste ich mich auf die Haupttypen beschränken. Eine kritische Bearbeitung aller Formen ist nur von Amerika aus möglich."

In 1933 Wiegand published a revisionary study on *Aster paniculatus* Lam. and related forms. It was intended primarily for eastern plants, as the following quotation indicates: "The study of this group of Asters as it occurs in the far west has not been as thorough, and the material has not been as complete as in the case of the eastern forms." The only species there treated with which we are concerned are *Aster coerulescens* and *Aster laetevirens*. The present writer has deviated from Wiegand's treatment chiefly in reducing *A. laetevirens* to varietal status under *A. coerulescens*, and in reducing *A. coerulescens* var. *Wootoni* to synonymy as a form intermediate to the var. *laetevirens*. Neither of these changes does great violence to Wiegand's concept, in view of the following quotations from his paper: Regarding *A. laetevirens*, "In all detailed measurements of parts of the head and florets it corresponds closely with *A. coerulescens*, to which it is evidently closely related." And regarding *A. coerulescens* var. *Wootoni*, "The status of this variety is not clear . . . Its aspect sometimes approaches that of *A. laetevirens*, but the involucre is like that of *A. coerulescens*."

Well over 100 names have been applied to forms of the group here considered. The difficulty of satisfactorily referring herbarium material to the proper places among these names first led the writer to become interested in the problem. The opinion has been slowly crystallizing in his mind that there are only a comparatively few genetically significant forms within the group, and that these hybridize freely. A considerable number of field hybrids have been observed, and herbarium material indicates that these were not exceptions to the rule. It seems evident, in fact, that wherever two species of the group are found growing together, hybrids may be expected, and that these hybrids are frequently fertile. In this connection it is interesting to note that Wiegand

(1928, 1933) has reached what appears to be substantially the same conclusion in his studies on eastern Asters. More recently, Wetmore and Delisle (1939) have experimentally produced hybrids between such externally dissimilar species as *A. ericoides* L. and *A. Novae-Angliae* L., and found them to simulate exactly herbarium specimens of *A. amethystinus* Nutt., which has long been suspected as being of hybrid origin. The same writers found that the F_1 hybrid between these two species, *A. ericoides* and *A. Novae-Angliae*, is not only fertile but can readily be back-crossed to either of the parents.

Such lack of genetic barriers brings about a complete obliteration of specific distinctions. If complete morphologic discontinuity were the sole criterion for the acceptance of species in this group, they could all be reduced to one species. Those units which are comparatively distinct from other units, and whose sub-units, if any, all share some common character or characters not found in closely related units, have been recognized as species. Geographic distribution of each of the units recognized as a species is fairly continuous, with the exception of *A. foliaceus*, which grows in Quebec, a thousand miles or more from the nearest known western station.

Following immediately on the question of specific criteria is the problem of intra-specific units. These, it seems to the writer, are of two general types: (1) those which have distinct geographical ranges of their own and intergrade with similar units where their ranges meet, and (2) those which are not, over most of their area, the sole representatives of their species. The former group I have treated as subspecies, the latter have been accepted as varieties.

Ecological subspecies have not been accepted. It seems to the writer that practically every genetically significant population will have its own ecological relationships, differing in greater or lesser degree from those of related populations occupying the same area. From the evolutionary viewpoint, forms occupying different habitats within the same region are more closely related than forms which are in the main geographically isolated from each other. Therefore the writer maintains that these ecological forms should be treated as units of less significance than geographical forms, and has disposed of them as varieties.

The criteria used in this treatment are mostly external and superficial, such as type of involucre, leaf shape and size, type of inflorescence, and pubescence. More technical characters of the achenes, disk corollas and pappus are in general too uniform to be of much value in distinguishing forms within this group. Type of involucre is probably the most important single criterion. Even this is highly variable, however, so that even the specialist cannot always determine a given specimen by examining the involucre. Degree of imbrication of the bracts, shape and apex of the bracts, and degree of leafiness are the most important features of involucre. Leaf shape and size, although admittedly inherently variable characters, have been found to be very helpful. *Aster Douglasii* and *A. chilensis* subsp. *typicus* run the gamut of variation in leaf shape, but the leaves in other species and intra-specific units are surprisingly uniform in proportions and even in absolute size. Only one species, *A. oregonus*, has a characteristic and consistently recognizable type of inflorescence, although that

character may be generally helpful in determining some of the other species. Distribution of pubescence is of considerable importance. The lines of pubescence decurrent from the leaf bases in *Aster coerulescens* are not exactly duplicated by any of the other species of the group, and the short uniform pubescence of *A. oregonus* is a consistent diagnostic character. Pappus color has a limited use, being fairly consistently reddish in *A. Douglasii* and usually whitish in the other species. Length of ligules is wholly unreliable, but color may be of some aid on occasion. White- and pink-flowered forms are apt to be consistently so, while other forms may run the complete range of coloration.

It has been generally accepted that aggregation and reduction have been major tendencies in the inflorescence of the *Compositae*. The writer arrived at this opinion independently, with respect to the *Asters* here considered, and suggests that in them these tendencies also extend to the leaves. In this group the following characters are believed to be primitive:

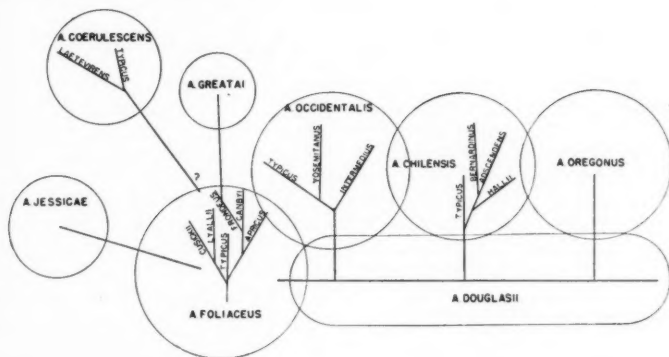
- (1) few heads, as opposed to many.
- (2) large heads, as opposed to small.
- (3) foliaceous involucre, as opposed to more chartaceous imbricated involucre.
- (4) few leaves, as opposed to many.
- (5) large leaves, as opposed to small.

Characters of pubescence and ligules are too variable, and other characters are too uniform, to be of much help in this regard in our forms.

Following the above criteria, *A. foliaceus* is necessarily selected as the most primitive species of the group. So far as the writer is aware, *A. foliaceus* does not show any distinctive difference from the other species of the group that cannot be placed under one of the five headings listed above, nor is any species more primitive than *A. foliaceus* in any of those headings. Thus we do not need to postulate the existence of some hypothetical species as the common ancestor to all our forms; *Aster foliaceus* seems to be it.

Which of the several forms of *A. foliaceus* to select as the oldest is more difficult. The varieties *Lyallii* and *frondeus* are ruled out by narrow phyllaries, while the variety *apricus* seems an unlikely choice because of its restricted alpine habitat. Remaining are the varieties *Cusickii*, *Canbyi*, and *typicus*. The largest-leaved, largest-headed form, with the most foliaceous involucre, is undoubtedly the variety *Cusickii*, but the presence of conspicuous pubescence and glabrous achenes, rather uncommon characters in the group, combined with its relatively limited range, preclude its selection. It is, however, the only form of the three which has its center of distribution in an area occupied by all the major species of the group. Rather similar to the variety *Cusickii*, but more nearly glabrous and centering in the Rocky Mountains proper, is the variety *Canbyi*. Its evident removal from the center of dispersion is enough to render it very unlikely as the choice. That leaves the variety *typicus*, most primitive in respect to number of heads, and the only form which reappears in Quebec. It is suggested that the monocephalous inflorescence may be merely a reduction due to a more rigorous habitat, and the reappearance in Quebec, while undoubtedly indicating antiquity, may perhaps be explained by its being the only one of the three forms formerly capable of withstanding the climate over the great northern arc that has been generally accepted as being the connecting link for such distri-

Simple linear descent among the species here considered is extremely difficult to find. It seems possible that the relationship is more nearly of a network type. Frequent fertile hybrids would of course tend to produce this type of relationship, or at least obscure the original derivation. A tentative phylogenetic arrangement is presented below.



Since the types of some of Greene's species are not available for loan, some of his names can be only provisionally disposed of. They have been tentatively placed in the lists of synonyms and indicated by question marks.

NY—New York Botanical Garden.

PA—Academy of Natural Sciences of Philadelphia.

PO—Pomona College, Claremont, California.

RY—University of Wyoming, Rocky Mountain Herbarium, Laramie.

UIS—University of Idaho, Southern Branch, Pocatello.

US—United States National Herbarium, Washington, D. C.

UT—Utah State Agricultural College, Intermountain Herbarium, Logan.

WS—Washington State College, Pullman.

Specimens from my own herbarium are designated as CR. Only a small proportion of the specimens seen are cited.

KEY

1. Pubescence of the stem and branchlets occurring in lines decurrent from the leaf bases, commonly neither uniform under the heads nor confined to the inflorescence.1. *Aster coerulescens*
1. Pubescence of the stem uniform, or if in lines, either uniform under the heads or very scanty and confined to the inflorescence.
 2. Involucres strongly graduated, at least the outer phyllaries obtuse, markedly shorter than the inner, and not foliaceous.
 3. Phyllaries with oblanceolate green tips, or if nearly wholly green, then narrowed at the bases.7. *Aster chilensis*
 3. Phyllaries nearly wholly green (at least the outer), not narrowed at the bases.8. *Aster occidentalis*
 2. Involucres not strongly graduated, or if so, the phyllaries markedly acute; phyllaries acute, or if obtuse, then enlarged and foliaceous.
 3. Outer phyllaries with conspicuous scarious margins near the bases, the chartaceous portions darkened, yellowish or brownish, not white; leaves commonly toothed; pappus usually reddish at maturity.5. *Aster Douglasii*
 3. Outer phyllaries with inconspicuous or no scarious margins, the chartaceous portions usually whitish or green-tinged (except in *A. Greatai*); leaves mostly entire (except in *A. Greatai*); pappus white or tawny.
 4. Inflorescence a long narrow leafy panicle with erect or stiffly ascending branches and numerous heads; stem pubescence mostly uniform throughout and short; leaves mostly over 7 times as long as broad.6. *Aster oregonus*
 4. Inflorescence few-headed, or if with many heads, then shorter, more open, and cymose-paniculate, often with much-reduced leaves; stem pubescence either uniform throughout or partially in lines; leaf shape variable.
 5. Middle stem leaves 1 cm. wide or more, mostly less than 7 times as long as broad.
 6. Phyllaries, and usually the whole herbage, soft-pubescent throughout.
 7. Leaves not markedly auriculate-clasping; involucre strongly graduated; plants of the vicinity of Pullman, Washington. 3. *Aster fessicæ*
 7. Leaves markedly auriculate-clasping; involucre usually not strongly graduated; plants of general distribution2. *Aster foliaceus*
 6. Phyllaries glabrous or nearly so on the backs, often ciliate on the margins or pubescent within; plant not soft-pubescent throughout.
 7. Leaves entire, the middle ones less than 2.5 cm. wide, or if wider,

- those of the inflorescence not conspicuously reduced; plants of general distribution.2. *Aster foliaceus*
7. Leaves frequently toothed, the middle ones very large, mostly over 2.5 cm. wide, the upper ones conspicuously reduced and bract-like; plants of the San Gabriel Mountains and vicinity.4. *Aster Greatai*
5. Middle stem leaves mostly less than 1 cm. wide and more than 7 times as long as broad.
6. Plant caespitose, decumbent, less than 2 dm. high; inner and sometimes outer phyllaries purple-tipped and -margined; alpine and subalpine plants2. *Aster foliaceus* var. *apricus*
6. Stems erect, commonly arising singly or in twos or threes from rhizomes, mostly over 2 dm. high; phyllaries usually not purple-margined, though often purple-tipped; mostly not alpine plants.8. *Aster occidentalis*

1. *ASTER COERULESCENS* DC. Prodrômus 5:235. 1836.

Stems caespitose, mostly 5-15 dm. high, green or more commonly reddish, at least the upper part pubescent in lines decurrent from the leaf bases, the pubescence commonly neither uniform under the heads nor scanty and confined to the inflorescence; leaves commonly glabrous or somewhat scabrous-hirsute on the upper surfaces, mostly glabrous on the lower surfaces, commonly scabrous-ciliate on the margins, entire or rarely somewhat toothed, sometimes prominently veined, but the areolae irregular and longer than broad; lower leaves linear to broadly oblanceolate, often narrowed to broad winged petioles, often deciduous before flowering; middle leaves linear to broadly lanceolate, 5-25 mm. broad, mostly 5-15 cm. long, scarcely auriculate, but sometimes rather clasping; upper leaves gradually or abruptly reduced, sometimes numerous and clothing the branchlets; heads medium-sized, the disks mostly 6-9 mm. high and 7-13 mm. broad, usually numerous in a long panicle and often somewhat secund on the branches; phyllaries usually scarious-margined toward the bases, acute, imbricate in several series, occasionally some of the outer ones loose, a little enlarged, and nearly wholly green; ligules 6-14 mm. long, white or pink to blue; achenes pubescent; pappus white or tawny. Streambanks and along ditches in the valleys, plains, and less commonly the mountains; Saskatchewan to Wisconsin and Texas, west to Idaho, Nevada, and southern California.

Type: Berlandier 510, November and December, 1828, Texas; isotype in Gray Herbarium.

KEY TO THE VARIETIES

1. Outer phyllaries mostly not much broader than the inner, the green tips not enlarged, less than one-fifth as wide as the length of the phyllaries.....a. var. *typicus*
1. Outer: phyllaries commonly broader than the inner, the green tips enlarged, at least one-fifth as wide as the length of the phyllaries.b. var. *lactevirens*

1a. *Aster coerulescens* DC. var. *typicus* Cronquist nom. nov.

Aster salicifolius Lam. var. *coerulescens* Gray Syn. Fl. 1(2):188. 1884.

Aster hesperius Gray Syn. Fl. 1(2):192. 1884.

PLATE I



Representative specimen of *Aster coerulescens* DC. var. *typicus* Cronquist.

Isotype of *Aster hesperius* Gray var. *Wooloni* Greene (= *A. coerulescens* var. *typicus*).

Aster hesperius Gray var. *Wooloni* Greene Bull. Torrey Club 29:645. 1898.

Aster ensatus Greene Pitt. 4:223. 1900.

Aster Wooloni Greene Leaflet 1:146. 1905.

Aster fluviatilis Osterh. Bull. Torrey Club 32:611. 1905.

Aster foliaceus Lindl. ex DC. var. *hesperius* Jepson Man. Pl. Calif. 1047. 1925.

Aster coerulescens DC. var. *Wooloni* Wiegand Rhodora 35:28. 1933.

Stems mostly 1 meter high or more; leaves mostly linear or narrowly lanceolate and more than 7 times as long as broad, sometimes broader, not at all clasping, the lower ones scarcely larger than those above and mostly deciduous before flowering; heads usually numerous, often secund on the branches; phyllaries linear or long-triangular, the tips scarcely at all enlarged, with rather prominent scarious margins mostly extending more than halfway from base to tip; ligules mostly blue, sometimes white or pinkish. Streambanks and along

ditches, mostly in the valleys and plains; North Dakota to Wisconsin and Texas, west to Idaho, Nevada, and southern California, north to Alberta and Saskatchewan.

Type: Berlandier 510, November and December, 1828, Texas; isotype in Gray Herbarium.

Aster hesperius Gray is apparently typical *A. coerulescens*, differing in no fundamental character. For further discussion see Wiegand's paper of 1933 on *Aster paniculatus* Lam. and related forms.

SPECIMENS SEEN: ALBERTA. Thomas Lake, August 19, 1906, Macoun 77062 (CO, G). Saskatchewan. Tramping Lake, Macoun 77063 (CO, G). ARIZONA. County undetermined: Tanner's Canyon, Huachuca Mountains, 1882, Lemmon & Lemmon 2905 (C, G). CALIFORNIA. Orange County: Newport Beach, Booth (C, CO, PO). San Bernardino County: two miles east of San Bernardino, September 30, 1934, Munz 13240 (CO, PO, UT); vicinity of San Bernardino, October 15, 1895, Parish 3878 (type of *A. ensatus* Greene) (C, G). San Diego County: 10 miles north of Santa Ysabel, 1926, Jones (PO). Tulare County: Visalia, September 26, 1921, Wiegand et al. 2498 (CO). COLORADO. Arapahoe County: south of Englewood, September 19, 1919, Clokey 3300 (G, RY). Jefferson County: Arvada, September 4, 1920, Clokey 3905 (G, WS). Weld County: New Windsor, September 3, 1905, Osterhout 3188 (G, RY). IDAHO. Canyon County: Caldwell, July 19, 1935, Boone 492 (RY). NEVADA. Lincoln County: Panaca, September 5, 1912, Jones (PO). NEW MEXICO. Dona Ana County: Mesilla valley, September 22, 1899, Woolon (C, PO, RY). Lincoln County: White Mountains, August 12, 1897, Woolon 329 (type of *A. hesperius* var. *Wooloni* Greene) (C, G, PO, RY). TEXAS. County undetermined: November and December, 1828, Berlandier 510 (type of *A. coerulescens* DC.) (G). UTAH. Cache County: mouth of Logan Canyon, August 8, 1938, Cronquist 1079B (UT); Logan, August 28, 1938, Cronquist 1097 (UT). 1097A (UT). Salt Lake County: Salt Lake City, August 26, 1879, Jones 1308 (G, PO, UT). WYOMING. Johnson County: Buffalo, September, 1900, Tweedy 3108 (WS).

1b. *Aster coerulescens* DC. var. *laetevirens* (Greene) Cronquist comb. nov.

Aster laetevirens Greene Pitt. 4:219. 1900.

Aster Osterhoutii Rydb. Bull. Torrey Club 31:654. 1904.

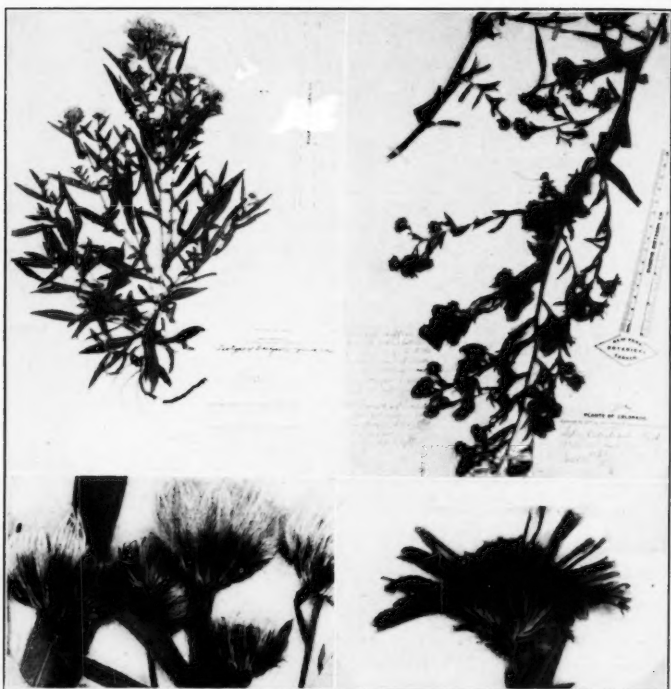
Brachyactis hybrida Greene Leaflet 1:147. 1905.

Stems a meter or more high, or sometimes shorter and only 5-10 dm. high; herbage rather markedly light green; middle leaves mostly 6-8 times as long as broad, sometimes narrower, commonly somewhat clasping; lower leaves mostly enlarged, oblanceolate, narrowed to broad winged petioles with clasping bases, often persistent till flowering; heads numerous or comparatively few, seldom secund on the branches; outer phyllaries usually broader than the inner, with prominent usually enlarged green tips and often with white midveins, the scarious margins inconspicuous and extending less than half-way from base to tip; ligules mostly white or pink, sometimes blue. Streambanks and along ditches in the valleys, plains, and less commonly in the mountains; northern New Mexico, Colorado, Wyoming, Idaho, northern Utah, and according to Wiegand (1933) Saskatchewan, North Dakota, and Arizona.

Type: Nelson 5293, September 7, 1898, Hutton's Lake, Albany County, Wyoming; isotype in Rocky Mountain Herbarium.

The variety *laetevirens* cannot be specifically separated from *A. coerulescens* var. *typicus*, as intergrades are very frequent. One of these intergrades has been

PLATE 2



Isotype of *Brachyactis hybrida* Greene
(= *A. coerulescens* var. *laetevirens*).

Isotype of *Aster Osterhoutii* Rydb.
(= *A. coerulescens* var. *laetevirens*).

named *A. Wootoni* Greene. The type specimen is an immature plant of the variety *typicus*, verging toward the var. *laetevirens*, but many other specimens that have been referred to *A. Wootoni* are thoroughly intermediate between the two varieties.

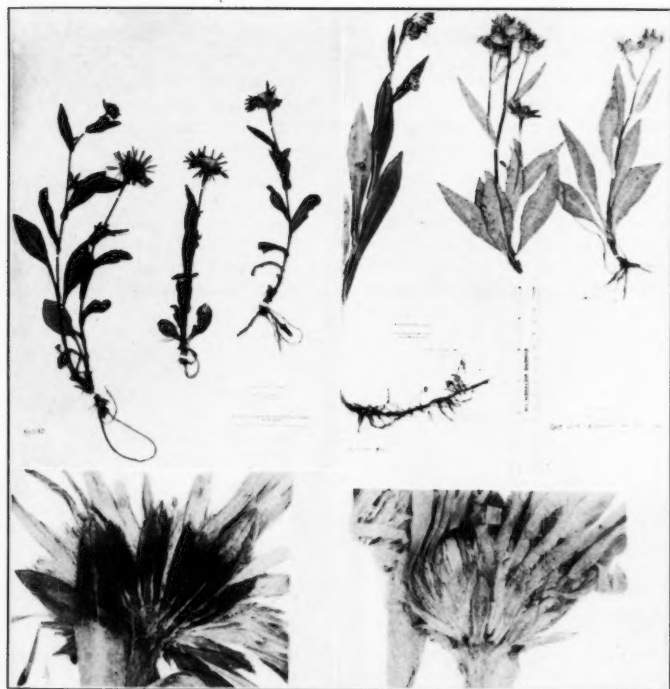
SPECIMENS SEEN: COLORADO. Gunnison County: Gunnison, August 16, 1901, *Baker* 817 (C, G, PO); Gunnison, August 27, 1901, *Baker* 937 (type of *Brachyactis hybrida* Greene) (US, WS). Montezuma County: Mancos, August 14, 1934, *Munz* 13116 (C, CO, PO). Weld County: New Windsor, September 29, 1899, *Osterhout* 2506 (type of *A. Osterhoutii* Rydb.) (NY, RY). IDAHO. Bannock County: Pocatello, September 4, 1938, *Cronquist* 1100 (UT). Fremont County: St. Anthony, August 30, 1899, *Henderson* 4826 (G). NEVADA: Elko County: Lamoille Creek, August 5, 1908, *Heller* 9304 (PA) (probably belongs here). NEW MEXICO. San Miguel County: near Pecos, August, 1908, *Standley* (G). UTAH. Cache County: Logan, October 3, 1936, *Cronquist* 400 (CR); mouth of Logan Canyon, August 8, 1938, *Cronquist* 1079A (UT); Logan, August 28, 1938, *Cronquist* 1094 (UT). WYOMING. Albany County:

East fork, August 25, 1894, *Nelson* 1118 (cotype of *A. laetevirens* Greene) (G). Johnson County: Buffalo, September, 1900, *Tweedy* 3100 (WS). Niobrara County: south of Lusk, August 24, 1931, *Osterhout* 7569 (PO).

2. *ASTER FOLIACEUS* Lindl. ex DC. Prodrum 5:228. 1836.

Stems caespitose, 1-10 dm. high, green or more commonly reddish, densely and uniformly pubescent to nearly glabrous, the pubescence often in lines, but if so either uniform under the heads or very scanty and confined to the inflorescence; leaves glabrous to densely soft-pubescent, mostly entire, the lower oblanceolate to obovate, usually narrowed to winged petioles or petioliform bases, often deciduous before flowering; middle stem leaves lanceolate to ovate or oblong, mostly 10-40 mm. wide (smaller in var. *apricus*) and 5-12 cm.

PLATE 3



Representative specimen of *Aster foliaceus* Lindl. ex DC. var. *typicus* Onno.

Type of *Aster adscendens* Lindl. ex DC. var. *Parryi* D.C. Eat. (= *A. foliaceus* var. *frondeus*).

long, $3\frac{1}{2}$ —6 or 7 times as long as wide; upper leaves gradually reduced, often passing into the phyllaries; heads medium-sized to large, the disks mostly 7-12 mm. high and 10-20 mm. broad, larger when fewer, 1-many, usually in a broad open cymose panicle; phyllaries loose or appressed, occasionally somewhat spreading, the outer wholly green, or white-margined at the bases, but without conspicuous scarious margins, as long as the inner or decidedly shorter, frequently leafy and surpassing the disk; ligules 10-20 mm. long, pink or rose-purple to blue or violet, rarely white; achenes glabrous or more commonly pubescent; pappus white or tawny, sometimes reddish. Mountains, woodlands, riverbanks, and along the seacoasts; central California north in the mountains to Alaska and the Aleutian Islands at 60 degrees north latitude, east to Wyoming, Colorado, and New Mexico, reappearing in Quebec.

Type not seen.

Aster foliaceus hybridizes very readily with both *A. Douglasii* and *A. occidentalis*, and to a probably lesser extent with the other species of the group. A goodly number of these hybrids have found their way into herbaria. This species includes more recognizable forms than any of the others here considered, all of these forms being characterized by broad leaves and usually leafy involucre. The several varieties represent very real entities, which are perhaps more easily recognized in the field than in the herbarium.

KEY TO THE VARIETIES

1. Stems erect, usually monocephalous; outer phyllaries nearly all foliaceous; plants of Alaska, British Columbia, and northern Washington.a. var. *typicus*
1. Stems usually not monocephalous, or if so mostly decumbent and ascending; outer phyllaries not always foliaceous; plants of Washington to California and eastward.
 2. Plant 2.5 dm. high or less, decumbent or ascending; phyllaries usually purple-tipped and -margined; mostly alpine plants.f. var. *apricus*
 2. Plant mostly over 2.5 dm. high, erect; phyllaries usually not purple-margined; mostly not alpine plants.
 3. Middle and upper stem leaves markedly auriculate-clasping; phyllaries frequently pubescent on the backs; stem frequently pubescent with spreading hairs.
 4. Phyllaries very narrow and acute or acuminate, the foliaceous ones, if present, linear or narrowly lanceolate and very acute.c. var. *Lyallii*
 4. Phyllaries broader, acute or obtusish, the foliaceous ones, if present, mostly broad and obtuse or acute.d. var. *Cusickii*
 3. Middle and upper stem leaves not markedly auriculate-clasping; phyllaries glabrous on the backs; stem not conspicuously pubescent, the hairs mostly appressed.
 4. Phyllaries narrow, acute or acuminate, the foliaceous ones, if present, linear or narrowly lanceolate and very acute; leaves usually rather thin.b. var. *frondeus*
 4. Phyllaries wider, obtuse or acutish, the foliaceous ones, if present, broadly lanceolate to ovate, rounded or obtuse to acutish; leaves usually rather thick.e. var. *Canbyi*

2a. *ASTER FOLIACEUS* Lindl. ex DC. var. *TYPICUS* Onno Bibl.

Botanica 106:7. 1932.

Mostly less than 6 dm. high; leaves glabrous or more commonly scabrous toward the margins and tips; mostly monocephalous, but occasionally bearing as many as half a dozen heads; phyllaries usually wholly green, the outer seldom much shorter than the inner, most of the outer usually enlarged and foliaceous, oblong, obtuse or acute, and sometimes purple-margined; phyllaries glabrous on the backs but often ciliate on the margins, the inner parts often soft-pubescent. Mountains, woods, rivers, and along the seacoast; northern Washington to Alaska and the Aleutian Islands at 60 degrees north latitude, apparently also in Quebec.

Type not seen.

PLATE 4

Type of *Aster foliaceus* Lindl. ex DC. var. *frondeus* Gray.Representative specimen of *Aster foliaceus* Lindl. ex DC. var. *frondeus* Gray.

This form occupies an area distinct from that occupied by any of the other western varieties, and may need to be given subspecific rank when the species as it occurs in Quebec is better understood. Plants from the Olympic Mountains of Washington are referable to this variety, although they tend to be taller and more robust than the more northern forms, and often bear several heads.

SPECIMENS SEEN: ALBERTA. Moraine Lake, September 19, 1937, McCabe 5247 (C). BRITISH COLUMBIA. Chilliwack valley, July, 1910, Macoun 26739 (G). ALASKA. Windham Bay, July 18, 1905, Baker 4932 (C, G, PO); Unalaska, August 14, 1899, Jepson 307 (G); Revillagigedo Island, August 6, 1915, Walker & Walker 898 (G, RY, US). MONTANA. Flathead County: 5 miles west of Logan Pass, Glacier National Park, July 8, 1934, Maguire et al. 15680 (CO, UT). WASHINGTON. Chelan-King County: Stevens Pass, August 16, 1893, Sandberg & Leiberger 759 (C, G, PO, RY, WS). Clallam County: Olympic Mountains, August, 1900, Elmer 2594 (PO, WS). Pierce County: Mount Tacoma (Rainier), Flett 53 (CO). Whatcom County: Skyline Ridge, August 20, 1937, Muenscher 8543 (C, CO, WS).

2b. *ASTER FOLIACEUS* Lindl. ex DC. var. *FRONDEUS* Gray

Syn. Fl. 12:193. 1884.

Aster adscendens Lindl. ex DC. var. *Parryi* Eaton Bot. King Exped. 5:139, 1871.

Aster foliaceus Lindl. ex DC. var. *Parryi* Gray Syn. Fl. 1(2):193. 1884.

Aster amplissimus Greene Proc. Acad. Philad. 1895. p. 550.

Aster frondeus Greene Proc. Acad. Philad. 1895. p. 551.

Aster glastifolius Greene Pitt. 4:218. 1900.

?*Aster exsul* Greene Pitt. 4:221. 1900.

Aster ciliomarginatus Rydb. Mem. N. Y. Bot. Gard. 1:392. 1900.

Aster diabolicus Piper Bull. Torrey Club 29:645. 1902.

Aster vaccinus Piper Bull. Torrey Club 29:646. 1902.

Mostly over 5 dm. high, sometimes lower; stem pubescent but not conspicuously so, the pubescence uniform only under the heads; leaves rather thin, glabrous, the petioles often strongly ciliate at the bases; lower leaves frequently enlarged, as much as 25 cm. long, usually persistent; heads several or many, rarely only 1; phyllaries glabrous without and usually also within, sometimes ciliate on the margins, linear, not narrowed at the bases, the outer ones as long as the inner ones and wholly green, or decidedly shorter and white-margined below, occasionally some enlarged and foliaceous, linear or lance-linear, very acute; achenes pubescent. Along streams and wet places; Cascade Mountains of northern Washington, south to central California, east to Wyoming and New Mexico.

Type: Watson 497, August, 1868, East Humboldt Mountains, Elko County, Nevada, in Gray Herbarium.

SPECIMENS SEEN: CALIFORNIA. Modoc County: Dismal Swamp, twenty mile creek, August 16, 1935, Wheeler 3875 (G). Nevada County: above Donner Lake, August 16, 1896, Sonne (C). Tuolumne County: Kennedy Meadow, August 11, 1915, Grant 220 (CO). COLORADO. Clear Creek County: Empire, September 3, 1878, Jones 730 (PO, UT). Gunnison County: Pitkin, September 2, 1917, Clakley 2979 (G, RY). County undetermined: latitude 39-41 degrees, 1862, Parry 417 (type of *A. adscendens* var. *Parryi* Eat.) (CO, G, PA). IDAHO. Clark County: above Spencer, August 29, 1937, Cronquist 878 (CR, UT); Webber Creek, August 19, 1939, Cronquist 1975 (UT). 1976 (UT), 1977 (UT); Ching Creek, August 23, 1939, Cronquist 2012

(UT), 2013 (UT). Custer County: Mackay, July 31, 1911, *Nelson & Macbride* 1496 (RY). MONTANA. Beaverhead County: Hell-Roaring Creek, July 18, 1937, *Cronquist* 721 (CR, UIS, UT). Park County: Electric Peak, August 20, 1897, *Rydberg & Bessey* 5128 (type of *A. ciliomarginatus* Rydb.) (NY, US). Lake County: Jocko Lakes, September 1, 1936, *Munz* 14565 (C, PO). NEVADA. Elko County: East Humboldt Mountains, August, 1868, *Watson* 497 (type of *A. foliaceus* var. *frondosus* Gray) (G). NEW MEXICO. County undetermined: Ponchuelo Creek, July 30, 1908, *Standley* 4583 (G). OREGON. Crook County: Squaw Creek, July 17, 1901, *Cusick* 2670 (type of *A. diabolicus* Piper) (C, CO, G, PO, RY, WS). Lane County: Quinn Meadows, August 8, 1898, *Coville & Applegate* 1058 (C). Malheur County: Cow valley, September 4, 1901, *Cusick* 2782 (type of *A. vaccinus* Piper) (C, CO, G, PO, RY, WS). Union County: Powder River Mountains, August, 1897, *Cusick* 1788 (C, CO, G, WS). UTAH. Cache County: Logan Canyon, October 15, 1938, *Cronquist* 1080 (UT); Logan, September 2, 1938, *Cronquist* 1100 (UT); Logan River, 25 miles east of Logan, September 3, 1933, *Maguire* 3834 (C, CO, RY, UT). Sevier County: Fish Lake, August 24, 1938, *Maguire* 16159 (UT). WASHINGTON. Okanogan County: Bonaparte Creek, August 18, 1933, *Fisher* 1384 (WS). WYOMING. Albany County: Wood's Creek, August 9, 1900, *Nelson* 8021 (C, PO, RY). Bighorn County: base of Medicine Mountain, July 23, 1896, *Williams & Williams* 3324 (G, RY, WS). Sheridan County: North Fork of Tongue River, August 29, 1935, *Williams* 2514 (C, G, WS). Teton County: String Lake, August 15, 1937, *Cronquist* 838A (CR).

2c. *Aster foliaceus* Lindl. ex DC. var. *Lyallii* (Gray) Cronquist comb. nov.

Aster Cusickii Gray var. *Lyallii* Gray Syn. Fl. 1(2):195. 1884.

Aster Hendersoni Fernald Bull. Torrey Club 22:273. 1895.

Aster ericaulis Rydb. Bull. Torrey Club 37:143. 1910.

Aster Kootenayi Nels. & Macbr. Bot. Gaz. 56:477. 1913.

Phyllaries linear, acuminate or very acute, the foliaceous ones when present narrow, tapering from base to apex, acuminate or very acute; resembling the var. *Cusickii*, but the leaves frequently smaller and not so conspicuously auriculate-clasping. Streambanks and moist woodlands; mountains of northern Idaho and adjacent parts of Oregon, Washington, Montana, and Canada.

Type: Lyall, August, 1861, between the Kootenay and the Pend Oreille, in Kew Herbarium; not seen.

SPECIMENS SEEN: BRITISH COLUMBIA. One mile south of Flathead Summit, September 10, 1937, *McCabe* 4979 (C). IDAHO. Bonner County: Priest Lake, 1901, *Piper* 3686 (G, WS). Kootenai County: St. Maries River, August 5, 1894, *Henderson* 2798 (type of *A. Hendersoni* Fernald) (CO, G, RY); valley of Traile River, August 9, 1892, *Sandberg, MacDougall & Heller* 877 (type of *A. ericaulis* Rydb.) (G, NY). Valley County: Payette Lakes, July 26, 1899, *Jones* (PO). MONTANA. Ravalli County: Lolo Hot Springs, August 2, 1925, *Kirkwood* 2121 (C, G, RY). Glacier National Park: July 16, 1934, *Osterhout* 8083 (RY). OREGON. Union County: 12 miles west of North Powder, August 17, 1915, *Peck* 3007 (G). WASHINGTON. Whitman County: Rock Lake, August 3, 1892, *Lake & Hull* 813 (G, WS).

2d. *Aster foliaceus* Lindl. ex DC. var. *Cusickii* (Gray) Cronquist comb. nov.

Aster Cusickii Gray Proc. Am. Acad. 16:99. 1881.

Mostly over 5 dm. high, frequently but not always densely pubescent throughout with conspicuous more or less spreading hairs; leaves very large and broad, the lower not markedly larger than those above, all with conspicuously auriculate-clasping bases; outer phyllaries wholly green or nearly so, some of them apparently always enlarged and foliaceous, ovate or broadly lanceolate,

PLATE 5



Type of *Aster eriocaulis* Rydb. (= *A. foliaceus* var. *Lyallii*).

Type of *Aster Hendersoni* Fernald (= *A. foliaceus* var. *Lyallii*).

obtuse or more commonly somewhat acute; achenes usually glabrate in age. Streambanks and moist woodlands; mountains of eastern Oregon to central Idaho and southeastern Washington.

Type: Cusick, July-August, 1878, along small subalpine streams, mountains of Union County, Oregon, in Gray Herbarium.

In its typical form this variety appears very distinct from *A. foliaceus*, but it grades directly into the other varieties that occur in its range, and cannot be specifically separated from them.

SPECIMENS SEEN: IDAHO. Boise County: Dry Buck, August 16, 1911, *Macbride* 1647 (C, G, PO, RY, UT, WS). Custer County: near Josephine Lakes, August 5, 1916, *Macbride* & *Payson* 3592 (G, RY). Idaho County: Coldwater Mountain, *Constance* & *Pennell* 1983 (C, UT, WS). OREGON. Union County: small subalpine streams, July-August, 1878, *Cusick* (type of *A. Cusickii* Gray) (G); Powder River

Mountains, August, 1897, *Cusick* 1797 (C, CO, WS): Powder River Mountains, August 26, 1898, *Cusick* 2105 (C, CO, G, PO, WS). Wallowa County: West fork of Wallowa River, September 3, 1927, *Keck* 353 (C, PO). WASHINGTON. Columbia County: Table Rock, September 23, 1928, *St. John* et al. 9647 (PO, WS). Yakima County: Big Klickitat River, September 1, 1903, *Colton* 1483 (WS).

2e. *ASTER FOLIACEUS* Lindl. ex DC. var. *CANBYI* Gray Syn. Fl. 12:193. 1884.

Aster foliaceus Lindl. ex DC. var. *Burkei* Gray Syn. Fl. 1(2): 193. 1884.

Aster Burkei Howell Fl. N. W. Am. 1:310. 1897.

Aster majusculus Greene Pitt. 4:215. 1900.

Aster Tweedyi Rydb. Bull. Torrey Club 31:655. 1904.

Aster Canbyi Vasey ex. Rydb. Fl. Colo. 354, 356. 1906.

Not *Aster Canbyi* Kuntze Rev. Gen. 315. 1891.

Aster phyllodes Rydb. Bull. Torrey Club 37:145. 1910.

Leaves rather thick, the lower ones seldom greatly enlarged, frequently deciduous; phyllaries narrowed toward the bases, the outer and sometimes also

PLATE 6



Type of *Aster foliaceus* Lindl. ex DC.
var. *Cusickii* (Gray) Cronquist.

Type of *Aster Tweedyi* Rydb. (= *A.*
foliaceus var. *Canbyi*).

the inner obtuse, some of the outer frequently enlarged and foliaceous, oblong to ovate, obtuse or acute; resembling the var. *frondeus*, but frequently shorter, passing readily into the var. *apricus*. Moist woodlands and hillsides; mountains of Washington to northern California, east to Wyoming, Colorado, and New Mexico.

Type: *Vasey* 262, October, 1868, White River, Colorado, in Gray Herbarium.

SPECIMENS SEEN: ARIZONA. Coconino County: Flagstaff, May-October, 1901, *Purpus* 8158 (C). County undetermined: Hart's Ranch, September, 1883, *Rusby* (cotype of *A. foliaceus* var. *Burkei* Gray) (G). COLORADO. Eagle County: Tennessee Pass, August 16, 1919, *Clokey* 3478 (C, G, PO, RY, UT, WS), 3487 (G, RY). Gunnison County: Crested Butte, August 13, 1901, *Baker* 812 (C, G, PO, RY, WS). Lake County: Everett, August 4, 1919, *Clokey* 3506 (G, PO, RY, UT, WS). Larimer County: east of Laramie River, August 28, 1897, *Osterhout* 2518 (cotype of *A. Tweedyi* Rydb.) (RY). County undetermined: White River, October, 1868, *Vasey* 262 (type of *A. foliaceus* var. *Canbyi* Gray) (G). IDAHO. Clark County: Ching Creek, August 23, 1939, *Cronquist* 2010 (UT). Fremont County: one mile east of Red Rock Pass, August 1, 1939, *Cronquist* 1903 (UT). MONTANA. Park County: 3.5 miles east of Cooke City, August 8, 1937, *Williams & Williams* 3774 (in part) (G). NEBRASKA. Kimball County: Lodgepole, near Kimball, August 12, 1891, *Rydborg* 165 (type of *A. phyllodes* Rydb.) (NY). NEW MEXICO. County undetermined: Mogollon Mountains, September 7, 1881, *Rusby* (cotype of *A. foliaceus* var. *Burkei* Gray) (G). OREGON. Grant County: Strawberry Lake, August, 1910, *Cusick* 3624 (in part) (WS). UTAH. Iron County: Cedar Breaks, August 7, 1934, *Maguire & Richards* 15736 (CO, UT). Salt Lake County: Alta, August 8, 1879, *Jones* 1226 (cotype of *A. foliaceus* var. *Burkei* Gray) (G, PO, UT). WASHINGTON. County undetermined: Simcoe Hills, September, 1880, *Howell* (cotype of *A. foliaceus* var. *Burkei* Gray) (G). WYOMING. Carbon County: Copperton, August 6, 1901, *Tweedy* 4096 (type of *A. Tweedyi* Rydb.) (NY). Platte County: Wheatland, July 14, 1891, *Buffum* 1842 (G, RY). Teton County: Teton Pass, August 16, 1937, *Cronquist* 825 (UIS, UT).

2f. *ASTER FOLIACEUS* Lindl. ex DC. var. *APRICUS* Gray. Syn. Fl. 12:193. 1884.

Aster apricus Rydb. Mem. N. Y. Bot. Gard. 1:396. 1900.

Aster incertus A. Nels. Bot. Gaz. 37:259. 1904.

Stems mostly less than 2.5 dm. high, caespitose and decumbent, from clustered rootstocks, densely and uniformly pubescent at least under the heads; leaves glabrous or slightly pubescent on the upper surfaces, scabrous-ciliate on the margins, small, the basal mostly 5-10 cm. long and 5-15 mm. wide, narrowed to petioliform bases, the middle ones 3-8 cm. long and 5-12 mm. wide; heads usually solitary, rarely as many as 7 in a contracted cyme; phyllaries glabrous on the backs but ciliate on the margins and soft-pubescent within, wholly green except for the purple tips and margins of the inner and sometimes the outer ones, the outer obtuse or acute and as long as the inner, or enlarged and surpassing them, the inner narrow, linear, acute or more commonly acuminate; ligules rose purple to deep violet; achenes pubescent. Alpine or subalpine stations in high mountains; southern British Columbia to northern California, east to Colorado and Wyoming.

Type: Wolf & Rothrock 521, 1873, Union Pass, Colorado, in Gray Herbarium.

SPECIMENS SEEN: BRITISH COLUMBIA. Chilliwack valley, August 29, 1901, *Macoun* 26378 (G). CALIFORNIA. Modoc County: Mount Bidwell, August 27, 1903, *Manning* 478 (C). COLORADO. Grand County: Berthoud Pass, July, 1903, *Tweedy* 5828 (RY). Summit County: Climax, August 7, 1919, *Clokey* 3504 (G, PO, RY). County undetermined: valley north of Gray's Peak, August, 1872, *Patterson & Beatty* (cotype of *A. foliaceus* var. *apricus* Gray) (G); Union Pass, 1873, *Wolf & Rothrock* 521 (type of *A. foliaceus* var. *apricus* Gray) (G). IDAHO. Clark County: head of Webber Creek, August 20, 1939, *Cronquist* 1990 (UT). Fremont County: Mount Jefferson, August 1, 1939, *Cronquist* 1881 (UT), 1925 (UT), 1909 (UT). OREGON. Grant County: Strawberry Lake, September 10, 1910, *Cusick* 3629 (WS). UTAH. Summit County: Lily Lake, 3 miles west of Bald Mountain, August 14, 1933, *Maguire et al.* 4280 (CO, RY, UT). WASHINGTON. Skamania-Yakima County: Mount Adams, 1882, *Howell* (cotype of *A. foliaceus* var. *apricus* Gray) (G); Mount Paddo (now Adams), September 1, 1882, *Suksdorf* 65 (cotype of *A. foliaceus* var. *apricus* Gray) (G).

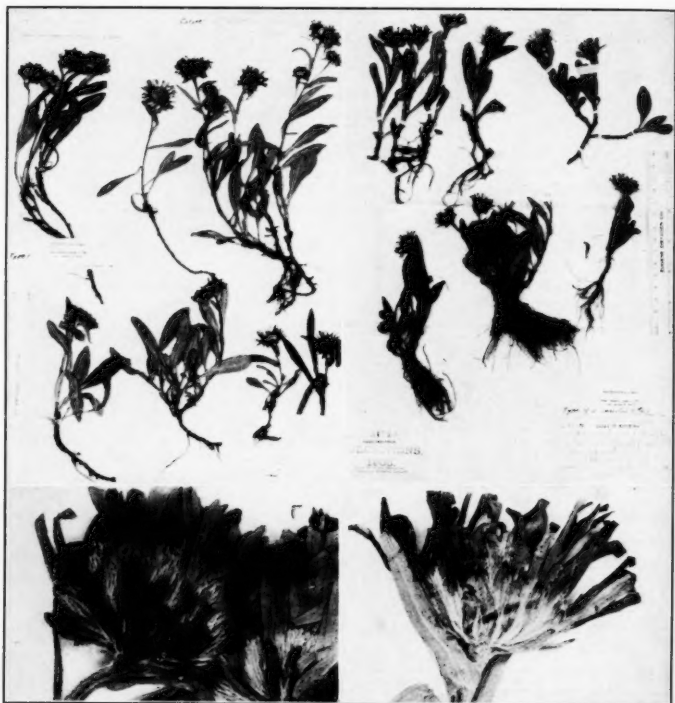
PLATE 7



Type of *Aster foliaceus* Lindl. ex DC.
var. *Canbyi* Gray.

Type of *Aster foliaceus* Lindl. ex DC.
var. *Burkei* Gray (= *A. foliaceus* var.
Canbyi).

PLATE 8



Type of *Aster foliaceus* Lindl. ex DC.
var. *apricus* Gray.

Type of *Aster incertus* A. Nels. (= *A.*
foliaceus var. *apricus*).

WYOMING. Albany County: Telephone Mines, August 2, 1900, *Nelson* 7924 (type of *A. incertus* A. Nels.) (C, CO, G, RY). Lincoln County: southeast of Smoot, August 5, 1923, *Payson et al.* 3733 (C, CO, PO, RY). Yellowstone Park: Yellowstone Lake, August 24, 1899, *Nelson & Nelson* 6644 (CO, G, PO, RY).

3. ASTER JESSICAE Piper *Erythea* 6:30. 1898.

Aster latahensis Henderson Contr. U. S. Nat. Herb. 5:201. 1899.

Aster mollis Rydb. Bull. Torrey Club 28:22. 1901 (at least as to cotype).

Stems tall, stout, mostly 8-15 dm. high, brown or straw-colored to reddish, apparently arising singly from stout rhizomes; the whole herbage densely and uniformly soft-pubescent throughout, the lower parts sometimes glabrate; lower cauline leaves oval to ovate, 7-12 cm. long, 2.5-4 cm. wide, abruptly contracted into winged petioles 3-8 cm. long, mostly deciduous before flowering; middle

stem leaves broadly lanceolate to oval, narrowed to slightly clasping and sometimes slightly auriculate bases, 6-13 cm. long, 15-25 mm. or even 30 mm. wide; upper leaves mostly rather numerous and reduced; heads mostly rather numerous in an open cymose panicle, medium-sized to large, the disks 8-12 mm. high and 10-18 mm. wide; involucre densely pubescent, more or less strongly graduated, the phyllaries appressed, acute or obtusish, the outer nearly wholly green, occasionally a few enlarged and foliaceous, scarious margins obscure or more commonly wanting; ligules 12-20 mm. long, mostly bluish; pappus tawny; achenes pubescent. Streambanks and low ground; Whitman County, Washington, and adjacent Idaho.

Type: Piper 1604, August, 1893, Pullman, Whitman County, Washington; isotype in Gray Herbarium.

PLATE 9

Topotype of *Aster jessicae* Piper.Isotype of *Aster greatai* Parrish.

Aster Jessicæ is apparently a rather uncommon endemic, being known from comparatively few collections. The occasional occurrence of enlarged herbaceous outer phyllaries shows its close phylogenetic connection to *Aster foliaceus*.

SPECIMENS SEEN: IDAHO. Latah County: 1 mile south of Troy, September 7, 1936, Constance 1811 (WS). WASHINGTON. Whitman County: Pullman, August, 1893, Piper 1604 (type of *A. Jessicæ* Piper, cotype of *A. mollis* Rydb.) (G).

4. *ASTER GREATAI* Parish Bull. So. Cal. Acad. 1:15. 1902.

Stems cespitose, green or sometimes reddish, usually tall and stout, 5-10 dm. high, with coarse uniformly scattered pubescence above, often glabrous below; leaves entire or frequently toothed, rather sparsely hirsute or strigose on the upper surfaces, usually more densely so on the lower surfaces; radical leaves oval, with blades 3-7 cm. long and 15-35 mm. wide, tapering into petioles 3-8 cm. long, but usually deciduous before flowering; lower stem leaves oblanceolate to broadly lanceolate, tapering to short winged petioles or petioliform bases, 10-20 cm. long and 2-5 cm. wide, but usually deciduous before flowering; middle stem leaves broadly lanceolate to oval, widest at or above the middle, 6-15 cm. long and 2-5 cm. wide, narrowed to slightly clasping or even somewhat auriculate bases; leaves of the inflorescence conspicuously reduced, often bract-like, seldom over 3 cm. long and 1 cm. wide; heads small to medium-sized, the disks 6-9 mm. high and 9-13 mm. broad, few or rather many in an open cymose panicle; phyllaries ciliate on the margins, loose, usually some squarrose or reflexed, only the tips green, the outer shorter than or sometimes nearly as long as the inner and then wholly green, scarious margins inconspicuous or wanting in the outer, more or less prominent on the inner; ligules pink or light purple, 8-15 mm. long; pappus white; achenes pubescent. Canyons of the San Gabriel and San Antonio Mountains, California, and vicinity.

Type: Greata, September 30, 1900, Eaton Canyon, Los Angeles County, California; isotype in University of California Herbarium.

It has been suggested that *A. Greatai* may be a form of *A. patula* L. escaped from cultivation (Hall, 1907). The writer is not familiar with that species, but from the description is inclined to think otherwise. The limited distribution need not be a cause of suspicion, as other endemics are found in the same area. It seems probable that it is derived directly from *A. foliaceus* by gradual change resulting from isolation.

SPECIMENS SEEN: CALIFORNIA. Los Angeles County: Eaton Canyon, September 30, 1900, *Greata* (type of *A. Greatai* Parish) (C). Los Angeles or San Bernardino County: Coldwater fork of Cattle Canyon, San Antonio Mountains, September 16, 1917, Johnston 1725 (C, G, PO, RY).

5. *ASTER DOUGLASII* Lindl. ex DC. Prodrômus 5:239. 1836.

?*Aster amplus* Lindl. ex DC. Prodrômus 5:236. 1836.

?*Aster limosus* Greene Pitt. 4:222. 1900.

Aster Elmeri Piper Bull. Torrey Club 29:645. 1902.

PLATE 10



Type of *Aster Elmeri* Piper (= *A. Douglassii*). Type of *Aster Butleri* Rydb. (= *A. Douglassii*).

Not *Aster Elmeri* Greene Pitt. 2:170. 1891.

Aster Wattii Piper Bull. Torrey Club 29:645. 1902.

Aster Butleri Rydb. Bull. Torrey Club 27:139. 1910.

Aster subcaudatus Rydb. Bull. Torrey Club 37:143. 1910.

Aster Umbachii Rydb. Bull. Torrey Club 37:144. 1910.

Aster okanoganus Piper Proc. Biol. Soc. Wash. 29:101. 1916.

Aster Carterianus J. K. Henry Ottawa Natur. 31:957. 1917.

Stems cespitose, mostly 4-10 dm. high, green or reddish, glabrous below, pubescent above, the longer hairs usually about 1 mm. long, uniformly distributed below the heads but often in lines farther down, frequently scanty and confined to the inflorescence and then not uniform under the heads; leaves glabrous, or more commonly scabrous at least toward the margins and tips, the lower ones oblanceolate and somewhat enlarged, narrowed to broad winged

petioles, 10-15 cm. long and 15-40 mm. wide, frequently deciduous; middle and upper leaves sessile, linear or lanceolate to oval, widest near the middle, slightly if at all auriculate, mostly 4-20 mm. wide, sometimes wider, 5-15 cm. long, mostly 4-12 times as long as wide, sometimes longer, usually toothed, but not uncommonly entire; inflorescence paniculate, with few or many heads, if many, usually long and narrow; heads medium-sized or small, mostly 5-10 mm. high and 6-15 mm. wide; phyllaries firm, thick, appressed, obtuse or acute, often markedly imbricate, glabrous on the backs, the chartaceous portions at the bases conspicuous, rather yellowish or brownish rather than white, the scarious margins usually broad and conspicuous, often fimbriate or ciliate on the edges; ligules 5-12 mm. long, pink to blue or violet; achenes more or less pubescent; pappus usually reddish at maturity. Streambanks, waste places, and along the seashore; Alaska to central California, occasional as far east as Idaho and Nevada, and, according to Blake (1925) in Wyoming.

Type not seen.

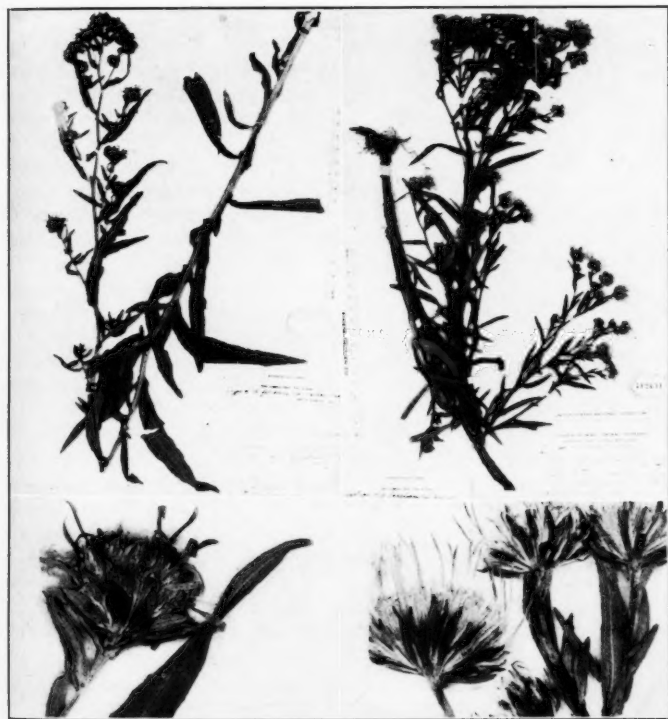
Aster Douglasii is perhaps the most variable species of the group here considered, and depends for its recognition on less tangible characters. Not one thing can be set down as a distinguishing characteristic always accompanying the species; rather it must be cut out on the basis of several rather inconstant characters. Perhaps the least satisfactory of these is the serration of the leaves, since the leaves are entire in a great many specimens; another is the reddish color of the pappus; a third, and most nearly consistent, is the conspicuous scarious margins of the outer and inner phyllaries, combined with the darkening of the chartaceous portions of the phyllaries. An annoying difficulty is that each of these characters is occasionally shown by other related species.

Aster Douglasii passes directly into three other species of the *A. foliaceus* group, namely *A. foliaceus*, *A. oregonus*, and *A. chilensis*. Specimens approaching *A. foliaceus* may usually be told from that species by the scarious margins of the phyllaries, a characteristic usually wanting in the outer phyllaries of *A. foliaceus*, and by the usually narrower leaves. Specimens approaching *A. oregonus* are most readily distinguished by the reddish pappus, more chartaceous involucre with scarious-margined phyllaries, firmer more reticulate leaves, and slightly longer and less uniform pubescence. Both *A. oregonus* and *A. foliaceus* have entire leaves, so that if the questionable specimen has serrate leaves it is almost certainly *A. Douglasii*. Forms of *A. chilensis* duplicate everything that characterizes *A. Douglasii*, and are distinguishable in such cases only by the strongly graduated involucre with obtuse outer phyllaries.

SPECIMENS SEEN: ALBERTA. Lake Louise region, August 23, 1902, Rosendahl 1089 (type of *A. subcaudatus* Rydb.) (NY); Quartz Creek, July 29, 1932, Raup & Abbe 4209 (G). BRITISH COLUMBIA. Cameron Lake, Vancouver Island, September, 1916, Carler 225 (WS), 226 (WS); Crescent, September 11, 1914, Henry 6923 (G, RY). ALASKA. Yes Bay, August 17, 1895, Howell 1632 (C, WS); Klawak Lake, Prince of Wales Island, September 12, 1915, Walker & Walker 1007 (G, RY, WS); Wrangell, 1915, Walker & Walker (RY). CALIFORNIA. Humboldt County: Stone Lagoon, September 13, 1923, Applegate 3992 (C). Monterey County: Castroville, June, 1908, Brandegee (C). Santa Clara County: Palo Alto, September, 1901, Abrams 2235 (RY). IDAHO. Bonner County: Clark's Fork valley below Weeksville, August 22, 1895,

Leiberg 1570 (C, G, PO, RY); Lake Pend d'Oreille, October 2, 1895, *Leiberg* 1662 (C, G, PO, RY). Kootenai County: Lake View, August 6, 1892, *Sandberg*, *MacDougall* & *Heller* 868 (G, PO). MONTANA. Flathead County: Lake MacDonald, August 20, 1901, *Umbach* 275 (type of *A. Umbachii* Rydb.) (NY). Glacier County: East entrance, Glacier National Park, July 14, 1934, *Osterhout* 8018 (RY). NEVADA. Elko County: Halleck, August, 1876, *Palmer* 150 (C). Washoe County: Wadsworth, August, 1876, *Palmer* 179 (C). OREGON. Clackamas County: Eagle Creek of Clackamas River, September 23, 1925, *Suksdorf* 3370 (C, G, PA, WS). Multnomah County: Bonneville, August 10, 1892, *Sheldon* 11087 (G, PO, WS). Umatilla County: Bingham Springs, October 7, 1908, *Cusick* 3328 (C, G, RY, WS). WASHINGTON. Clallam County: Olympic Mountains, July, 1900, *Elmer* 2635 (WS). Okanogan County: Sinlahekin basin, August, 1897, *Elmer* 571 (type of *A. Elmeri* Piper) (US). Spokane County: Spokane River, June, 1897, *Elmer* 685 (PO, RY). Whatcom County: Woodlawn, August 23, 1937, *Muenschner* 8532 (CO, WS). Yakima County: North Yakima, August, 1895, *Watt* (type of *A. Wattii* Piper) (WS).

PLATE II



Type of *Aster foliaceus* Lindl. ex DC.
var. *Eatonii* Gray (= *A. oregonus*).

Isotype of *Aster lonchophyllus* Greene
(= *A. oregonus*).

6. *ASTER OREGONUS* (Nutt.) T. & G. Fl. N. Am. (as *A. oregonus*)
2:163. 1841.

- Tripolium oregonum* Nutt. Trans. Am. Phil. Soc. n. ser. 7:296. 1840.
Aster occidentalis (Nutt) T. & G. var. *scabriusculus* Gray Syn. Fl. 1(2):192. 1884.
Aster foliaceus Lindl. ex DC. var. *Eatoni* Gray Syn. Fl. 1(2):194. 1884.
Aster Eatoni Howell Fl. N. W. Am. 1:310. 1897.
Aster fulcratus Greene Pitt. 4:217. 1900.
Aster proximus Greene Pitt. 4:220. 1900.
Aster cordalenus Henders. Bull. Torrey Club 27:345. 1900.
Aster lonchophyllus Greene Leaf. 1:146. 1905.
Aster roseolus Rydb. Bull. Torrey Club 37:141. 1910.
Aster Mearnsii Rydb. Bull. Torrey Club 37:144. 1910.

Stems caespitose, mostly 4-10 dm. high, usually red or reddish, usually glabrous below, uniformly short-pubescent above with crisp curled appressed or spreading hairs less than $\frac{1}{2}$ mm. long, the pubescence occasionally denser in lines decurrent from the leaf bases, but still extending about the stem; leaves glabrous, or more commonly scabrous at least toward the margins and tips, entire or rarely somewhat toothed, the lower ones usually deciduous, if persistent oblanceolate and somewhat enlarged, more or less narrowed at the bases, 10-15 cm. long and 1-2 cm. wide; middle and upper leaves sessile, linear or lanceolate, seldom much contracted at the bases, slightly if at all auriculate, mostly 4-10 mm. wide, sometimes wider, 5-15 cm. long, mostly 7-13 times as long as wide, sometimes short and broad, 4-6 cm. long and 5-12 mm. wide, or long, linear, and very narrow, as much as 25 times as long as wide; inflorescence a long narrow leafy panicle with numerous heads borne on erect or stiffly ascending branches; heads medium-sized or rather small, the disks mostly 5-10 mm. high and 6-15 mm. wide; phyllaries loose, thin, seldom much imbricate, usually at least some of the outer and also some of the inner reflexed, obtuse or acute, glabrous on the backs but often ciliate on the margins, the chartaceous portions at the bases white or nearly so, not darkened, the scarious margins usually narrow and inconspicuous, or absent; ligules 5-12 mm. long, white or flesh-colored to dark pink, very rarely bluish; achenes more or less pubescent; pappus white or whitish, rarely somewhat tawny. Streambanks and wet places in the mountains and valleys; southern British Columbia and Alberta to central California, east to Wyoming, Colorado and New Mexico; rare west of the Cascade Mountains, common elsewhere.

Type not seen.

Aster oregonus is one of the most satisfactory species of the group, being characterized by the long inflorescence, short uniform pubescence, comparatively narrow leaves, and pink or white ligules. It is most apt to be confused with *A. Douglasii*, some forms of which pass directly into it, although some other forms of that species are very different from it.

The writer has observed field hybrids between *A. oregonus* and two varieties of *A. foliaceus*, and herbarium specimens whose characters indicate hybridization with other species have been seen.

A determined attempt was made to separate the form which has been called

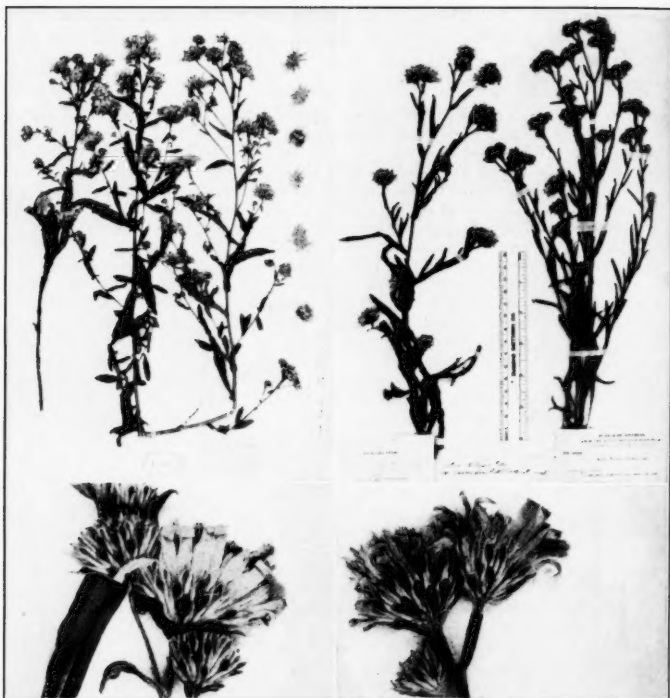
A. Eatonii (Gray) Howell at least varietally from *A. oregonus*, but without success. The larger heads and wider leaves on which the distinction of *A. Eatonii* presumably rests seem to be merely the result of growth in a more favorable habitat, and are entirely inconstant.

SPECIMENS SEEN: ALBERTA. Banff district, July 17, 1928, *Brinkman* 3436 (CO). BRITISH COLUMBIA. Vancouver Island, August 8, 1887, *Macoun* 61 (G); Donald, Columbia valley, July 13, 1885, *Macoun* 1021 (G). ARIZONA. Coconino County: Flagstaff, May-October, 1900, *Purpus* 8113 (C). CALIFORNIA. Butte County: Jonesville, August 26, 1930, *Copeland* 487 (C, PO, RY, UT). Modoc County: Forestdale, August 30, 1898, *Baker* (C, RY). Nevada County: Soda Springs, July, 1881, *Jones* (PO). Sierra County: 1874, *Lemmon* h84 (cotype of *A. foliaceus* var. *Eatonii* Gray) (G). Tuolumne County: Soda Springs, Kennedy Meadow, September 3, 1915, *Grant* 450 (PO). COLORADO. Gunnison County: Crested Butte, August 13, 1901, *Baker* 805 (type of *A. lonchophyllus* Greene) (G, RY, US, WS). Mineral County: near Pagosa Peak, August 12, 1899, *Baker* 638 (type of *A. fulcratus* Greene) (C, G, RY). IDAHO. Ada County: Boise, August 22, 1911, *Nelson* and *Macbride* 281 (G, RY). Bannock County: Camp Tendoy, August 27, 1939, *Cronquist* 2028 (UT). Clark County: Sheridan Creek, July 31, 1937, *Cronquist* 778a (CR, UT); Beaver Creek, above Spencer, August 29, 1937, *Cronquist* 876 (CR, UT); Ching Creek, August 23, 1939, *Cronquist* 2008 (UT). Fremont County: Henry's Lake, July 28, 1939, *Cronquist* 1882 (UT). Kootenai County: Lake Couer d'Alene, August 22, 1897, *Henderson* 2992 (type of *A. cordalensis* Henderson) (CO, G, WS). MONTANA. Park County: Emigrant Gulch, August 23, 1897, *Rydberg & Bessey* 5121 (G, RY, WS). Ravalli County: Rock Creek near Little Hogback Creek, August 9, 1933, *Hitchcock* 2105 (PO, RY). NEVADA. Clark County: Charleston Mountains, September 12, 1925, *Jaeger* (C, PO). Elko County: East Range of Humboldt Mountains, 1865, *Torrey* 205 (cotype of *A. foliaceus* var. *Eatonii* Gray) (G); Virginia Mountains, August, 1867, *Watson* 505 (type of *A. foliaceus* var. *Eatonii* Gray) (G). Washoe County: Steamboat Springs, September 18, 1911, *Heller* 10370 (C, G, PO). County undetermined: northern Nevada, 1868, *Watson* 506 (type of *A. occidentalis* var. *scabriusculus* Gray) (G). OREGON. Harney County: Burns-Drewsey road, August 13, 1901, *Cusick* 2780 (C, G, PO, RY, WS). Klamath County: near Fort Klamath, August 7, 1894, *Leiberg* 676 (C, G). Morrow County: Rhea Creek, September 11, 1894, *Leiberg* 892 (C, G). Union County: streambanks, August, 1897, *Cusick* 1820 (C, G, WS). Wallowa County: Wallowa River near lake, September 1, 1900, *Cusick* 2488 (C, G, PO, RY, WS). Washington County: wet places, August, 1880, *Howell* (G). UTAH. Cache County: Logan, July 16, 1938, *Cronquist* 1021 (UT); Logan Canyon, August 15, 1938, *Cronquist* 1081 (UT); Logan, August 28, 1938, *Cronquist* 1096 (UT). Iron County: 12 miles east of Cedar City, August 5, 1934, *Maguire & Richards* 15714 (UT). County undetermined: Rabbit Valley, August 18, 1875, *Ward* 605 (cotype of *A. occidentalis* var. *scabriusculus* Gray) (G, PA). WASHINGTON. Kittitas County: Beverly Creek, September 2, 1933, *Thompson* 10043 (C, G). Okanogan County: Loomiston, August, 1897, *Elmer* 614 (RY, WS). Spokane County: Spokane River at Spokane, September 3, 1896, *Piper* 2377 (G, WS). WYOMING. Albany County: Laramie, September 15, 1899, *Nelson* 6780 (RY). Sublette County: 15 miles northeast of Bon-durant, August 15, 1922, *Payson & Payson* 3082 (C, G, PO, RY). Yellowstone National Park: Mammoth Hot Springs, October 11, 1902, *Mearns* 4806 (type of *A. Mearnsii* Rydb.) (NY).

7. *ASTER CHILENSIS* Nees *Aster* 133. 1832.

Stems erect or ascending, more or less caespitose, usually over 3 dm. high except in depauperate or alpine forms, straw-colored or brown, sometimes green or reddish, uniformly pubescent at least under the heads, the pubescence often more or less in lines on the lower part of the stem; leaves usually entire, occasionally somewhat crenate-toothed, glabrous or more commonly more or less

PLATE 12



Representative specimen of *Aster chilensis* Nees ssp. *typicus* Cronquist.

Cotype of *Aster Nelsonii* Greene. (= *A. chilensis* ssp. *adscendens*).

pubescent, sometimes densely so, the lower leaves usually oblanceolate and narrowed to winged petioles or petioliform bases, but usually deciduous except in smaller plants; middle and upper leaves sessile, sometimes narrowed toward the bases, often somewhat auriculate, linear to obovate or oval, 2-10 cm. long and 2-20 mm. wide; inflorescence panicle, racemose, or cymose, occasionally monocephalous; heads small to medium-sized, the disks 5-11 mm. high and 6-15 mm. wide; phyllaries mostly erect and appressed, glabrous or pubescent, often ciliate on the margins, strongly imbricate in 3-4 series, the outer obtuse with oblanceolate green tips, the inner obtuse to acute or acuminate, sometimes purple-margined, the chartaceous portions at the bases usually white but sometimes darkened, the scarious margins of the outer obscure or occasionally prominent; ligules white to blue, pink, or violet, 5-15 mm. long; achenes more or less pubescent; pappus white or whitish, sometimes tawny or even reddish.

Dry ground, plains, saline marshes, along irrigation ditches, streambanks, hillsides, and woodland; Washington to California, east to Saskatchewan and New Mexico.

Type not seen.

KEY TO THE SUBSPECIES

1. Inflorescence conspicuously divaricate-bracteate, the bracts mostly obtuse or acutish and 2-4 times as long as wide; ligules mostly white; leaves linear; plants of Oregon and Washington.c. subsp. *Hallii*
1. Inflorescence not conspicuously divaricate-bracteate, the bracts, if present, mostly erect, more than 4 times as long as wide, and markedly acute; ligules mostly blue or pinkish, rarely white; leaves linear to lanceolate or oval.
2. Innermost phyllaries obtuse or merely acutish; middle stem leaves frequently over 1 cm. wide and less than 7 times as long; plants of California and southern Oregon, west of the Cascade and Sierra Nevada summits.a. subsp. *typicus*
2. Innermost phyllaries acuminate or distinctly acute; middle stem leaves mostly less than 1 cm. wide and more than 7 times as long; plants of the Rocky Mountains and Great Basin, east of the Sierra Nevada.b. subsp. *adscendens*

7a. *Aster chilensis* Nees subsp. *typicus* Cronquist nom. nov.

Aster chilensis Nees *Aster* 133. 1832.

Aster Menziesii Lindl. ex DC. *Prodromus* 5:243. 1836.

Aster Chamissonis Gray ex. Torr. in Wilkes Exped. 17:341. 1874.

?*Aster invenustus* Greene Man. Bot. San Francis. Bay 179. 1894.

?*Aster lentus* Greene Man. Bot. San Francis Bay 180. 1894.

?*Aster sonomensis* Greene Man. Bot. San Francis. Bay 180. 1894.

?*Aster militaris* Greene Proc. Acad. Phil. 1895. p. 550.

?*Aster chilensis* Nees var. *invenustus* Jeps. Fl. W. Middle Calif. 566. 1901.

?*Aster chilensis* Nees var. *lentus* Jeps. Fl. W. Middle Calif. 566. 1901.

?*Aster chilensis* Nees var. *sonomensis* Jeps. Fl. W. Middle Calif. 567. 1901.

Plant nearly glabrous to densely pubescent throughout; middle stem leaves linear or more commonly lanceolate to oblong or oval or obovate, commonly 1 cm. wide or more and less than 7 times as long, entire or obscurely crenate, often more or less auriculate; branches of the inflorescence often clothed by bracts, but these appressed, narrow, and acute; innermost phyllaries obtuse or merely acutish; ligules blue to pink or violet. Waste places, saline marshes, woodlands, and hillsides; California and southern Oregon, west of the Cascade and Sierra Nevada summits.

Type not seen.

The form which has been called *Aster Menziesii* Lindl. is apparently typical *A. chilensis*, although a comparatively simple, narrow-leaved, and heavily pubescent form of the species has been commonly referred to it. A drawing of the type specimen has been seen, and it apparently differs in no essential way from the typical form of *A. chilensis*.

SPECIMENS SEEN: CALIFORNIA. Alameda County: Berkeley, July-September, 1906. Walker 459 (C, PO, RY). Butte County: Chico-Hamilton road, 6 miles from Chico, September 3, 1914, Heller 11760 (C, G). Marin County: Reys peninsula, October 22, 1933, Ewan 8054 (C, PO). San Diego County: Palomar Mountain, September 14, 1922, Spencer 1993 (PA). San Mateo County: southwest of Woodside, October 15,

1930, *Keck* 989 (G, PO). Santa Clara County: foothills west of Los Gatos, September 12, 1904, *Heller* 7538 (C, G, RY). Siskiyou County: near Orofino, August 29, 1908, *Butler* 289 (C). County undetermined: drawing of type of *A. Menziesii* Lindl. in Herb. Kew (C). OREGON. Benton County: Corvallis, July 23, 1926, Scullen (C).

PLATE 13



Type of *Aster Hallii* Gray (= *A. chilensis* ssp. *Hallii*).

Type of *Aster chilensis* Nees ssp. *adscendens* (Lindl. ex DC.) Cron. var. *bernardinus* (Hall) Cron.

7b. *Aster chilensis* Nees subsp. *adscendens* (Lindl. ex DC.)
Cronquist comb. nov.

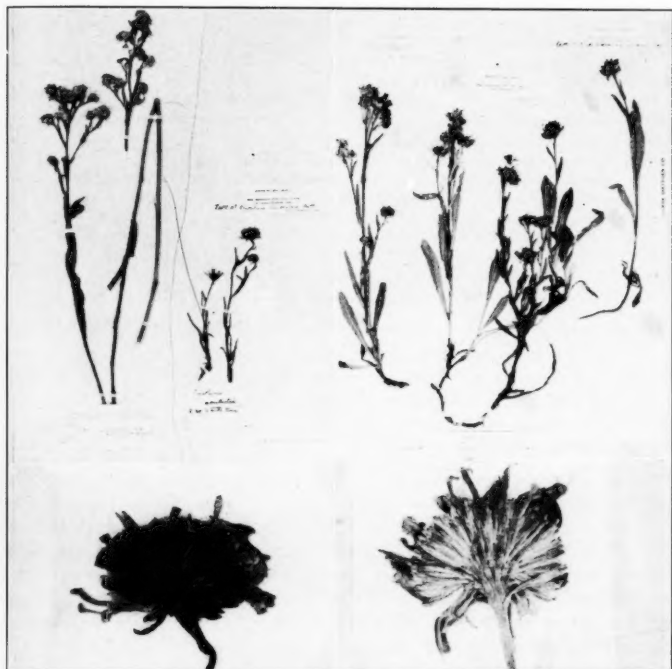
Aster adscendens Lindl. ex DC. Prodomus 5:231. 1836.

Plant nearly glabrous to densely pubescent throughout; middle stem leaves mostly less than 1 cm. wide and more than 7 times as long as wide, entire, not at all auriculate; inflorescence usually not conspicuously bracteate, the bracts, if present, narrow, markedly acute, and mostly erect; inner phyllaries narrow, acuminate to strongly acute; ligules blue to pinkish or violet, rarely white. Dry

ground, plains, saline marshes, along irrigation ditches, streambanks, hillsides, and woodland; southeastern Washington to southern California, chiefly east of the Cascade and Sierra Nevada summits; east to Saskatchewan and New Mexico.

Type not seen.

PLATE 14



Type of *Aster occidentalis* (Nutt.) T. & G. var. *typicus* Cronquist.

Type of *Aster adscendens* Lindl. ex DC. var. *Fremonti* T. & G. (= *A. occidentalis* var. *typicus*).

KEY TO THE VARIETIES

1. Phyllaries and the whole herbage conspicuously pubescent with long spreading hairs; plants of southern California. 2. var. *bernardinus*
1. Phyllaries and herbage glabrous, or if pubescent the hairs mostly short or appressed; plants of the Rocky Mountains, Great Basin, and eastern Oregon, as well as southern California 1. var. *euadscendens*

7b1. *Aster chilensis* Nees subsp. *adscendens* (Lindl. ex DC.) Cronquist
var. *euadscendens* Cronquist nom. nov.

- Aster adscendens* Lindl. ex DC. Prodrum 5:231. 1836.
Aster denudatus Nutt. Trans. Am. Phil. Soc. n. ser. 7:292. 1840.
Aster denudatus Nutt. var. *ciliatifolius* Nutt. Trans. Am. Phil. Soc. n. ser. 7:293. 1840.
Aster ramulosus Nutt. Trans. Am. Phil. Soc. n. ser. 7:293. 1840.
Aster adscendens Lindl. ex DC. var. *denudatus* T. & G. Fl. N. Am. 2:111. 1841.
Aster Nuttallii T. & G. Fl. N. Am. 2:126. 1841.
Aster subracemosus Rydb. Mem. N. Y. Bot. Gard. 1:394. 1900.
 ? *Aster distichophyllus* Greene Pitt. 4:213. 1900.
Aster violaceus Greene Pitt. 4:214. 1900.
Aster pratincola Greene Pitt. 4:215. 1900.
Aster spithameus Greene Pitt. 4:217. 1900.
Aster Nelsonii Greene Pitt. 4:219. 1900.
 ? *Aster vallicola* Greene Pitt. 4:219. 1900.
 ? *Aster limoniifolius* Greene Pitt. 4:222. 1900.
Aster oxylepis Greene Pitt. 4:223. 1900.
Aster griseolus Rydb. Bull. Torrey Club 31:653. 1904.
Aster Underwoodii Rydb. Bull. Torrey Club 31:653. 1904.
Aster orthophyllus Greene Leaff. 1:146. 1905.
Aster griseus Greene Leaff. 1:147. 1905.
 ? *Aster halophilus* Greene Leaff. 2:8. 1909.
 ? *Aster leucopsis* Greene Leaff. 2:8. 1909.
Aster subgriseus Rydb. Fl. Rocky Mts. 884. 1917.
Aster deserticola Macbr. Contr. Gray Herb. n. ser. 55:36. 1918.

Plant sparingly hairy to densely pubescent, if densely so, then the hairs mostly short, curled, and more or less appressed; leaves linear to lanceolate. Ditchbanks and waste places, less commonly in the mountains; eastern Oregon to southern California, mostly east of the Cascade and Sierra Nevada summits, east to Saskatchewan and New Mexico.

Type not seen.

Of all the segregates that have been proposed from this variety, only *Aster griseus* Greene is distinctive enough to warrant comment. It is a fairly common form in the mountains of Colorado, rather densely pubescent with short curled hairs, and having more or less habitual unity and similarity of appearance between specimens. The quantity of pubescence is entirely inconstant, however, and some specimens with exactly the habit of *A. griseus* are nearly glabrous. The inconstancy of the only distinctive character, pubescence, and the general polymorphy of the variety and species as a whole, indicate that it is not worthy of nomenclatural recognition.

SPECIMENS SEEN: ALBERTA. Belly River, July 26, 1895, Macoun 10247 (G). CALIFORNIA. Eldorado County: Glen Alpine Canyon, near Lily Lake, August 20, 1930, Abrams 12571 (C, G). Los Angeles County: Prairie Fork, San Gabriel River, August 23, 1917, Johnson 1640 (C, PO). Modoc County: Goose Lake valley, June, 1894, Austin 207 (C). Riverside County: Hemet valley, San Jacinto Mountains, October 16, 1932, Munz 12838 (C, CO, PO). San Bernardino County: Mohave desert, October 3, 1917, Spencer 629 (type of *A. deserticola* Macbr.) (NY, PO). Siskiyou County: Deetz station, August 25, 1914, Heller 11713 (C, G, CO). COLORADO. Archuleta County: Pagosa Springs, August, 1899, Baker 641 (C, G, RY). Chaffee County: Buena Vista, August 9, 1919, Clokey 3508 (G, RY, WS). Clear Creek County: Georgetown, July 11, 1878, Jones 439 (G, PO, UT). Gunnison County: Gunnison, July 23, 1901, Baker 545 (type or cotype of *A. orthophyllus* Greene) (RY); Doyle's,

July 28, 1901, *Baker* 630 (C, G, PO, RY, WS); Doyle's, July 28, 1901, *Baker* 632 (type of *A. griseus* Greene) (C); Mount Harvard, 1896, *Clements* 37 (type of *A. griseolus* Rydb.) (NY). Montrose County Cerro Summit, August 1, 1901, *Baker* 688 (C, G, PO, RY, WS); Bedrock, August 2, 1912, *Walker* 397 (G, RY, WS). Ouray County: Ironton Park, September 11, 1901, *Underwood & Selby* 318 (type of *A. Underwoodii* Rydb.) (NY). San Miguel County: near Trout Lake, August 21, 1924, *Payson & Payson* 4178 (C, G, RY). Summit County: Breckenridge, August 24, 1896, *Cowen* 2688 (G, RY, WS). IDAHO. Bannock County: Camp Tendoy, July 31, 1936, *Cronquist* 339 (CR); Pocatello, August 8, 1936, *Cronquist* 348 (CR). Bear Lake County: Montpelier, August 4, 1911, *Nelson & Macbride* 1613 (C, G, RY, UT, WS). Canyon County: Falk's store, July 8, 1911, *Macbride* 1039 (C, G, RY). Clark County: Sheridan Creek, July 31, 1937, *Cronquist* 778C (CR); east of Argora, August 19, 1939, *Cronquist* 1952 (UT). Fremont County: Buffalo Forest Camp, July 27, 1939, *Cronquist* 1800 (UT). Nez Perce County: Lewiston, October 10, 1903, *Beattie* 2305 (WS). Owyhee County: Boulder Creek, July 31, 1910, *Macbride* 506 (C, G, RY, WS). Power County: American Falls, July 28, 1911, *Nelson & Macbride* 1389 (C, G, RY, WS). MONTANA. Deerlodge County: Anaconda, October 2, 1906, *Blankinship* (C, PO, RY). Gallatin County: Bozeman, September 10, 1901, *Jones* (C, G, RY, UT). Lewis & Clark County: Helena, September 8, 1890, *Kelsey* (type of *A. subracemosus* Rydb.) (NY). NEVADA. Elko County: Blaine, August 23, 1913, *Heller* 11123 (C, G, PA). Esmeralda County: Davis ranch, August 18, 1880, *Shockley* 568 (C). Washoe County: Little Valley, August 14, 1902, *Baker* 1474 (C, G, PO, RY). NEW MEXICO. Rio Arriba County?: northern New Mexico, September, 1899, *Baker* 642 (PO, RY). OREGON. Harney County: 25 miles north of Burns, July 16, 1936, *Thompson* 13296 (PA, WS). Josephine County: 2 miles west of Eagle Point, *Heller* 12973 (C, CO). County undetermined: bars and banks of the Snake River, September 27, 1898, *Cusick* 2122 (C, CO, PO, WS). UTAH. Cache County: Tony Grove Lake, August 15, 1938, *Cronquist* 1085 (UT); 2 miles northwest of college, October 9, 1932, *Maguire* 3840 (C, CO, RY, UT). Duchesne County: vicinity of Myton, September 23, 1932, *Richards & Wann* (CO, UT). Grand County: Mill Canyon, La Sal Mountains, August 17, 1934, *Maguire & Richards* 15737 (CO, UT). Iron County: 3 miles north of Cedar Breaks Lodge, August 12, 1938, *Hitchcock* et al. 4606 (C, RY, UT, WS). Salt Lake County: Alta, August 4, 1879, *Jones* 1180 (G, PO, UT). Washington County: Pine valley campground, August 29, 1937, *Gierisch* 576 (UT). WASHINGTON. Whitman County: Wawawai, September, 1903, *Piper & Beattie* (WS). WYOMING. Albany County: Sheep Mountain, September 2, 1903, *Goodding* 2093 (C, CO, G, RY); Laramie, September 15, 1899, *Nelson* 6868 (cotype of *A. Nelsonii* Greene) (CO, G, RY); Bacon's Ranch, August 15, 1903, *Nelson* 8926 (C, CO, G, RY). Big Horn County: Shell Creek Canyon, near Grouse Creek, July 8, 1936, *Williams* 3824 (G, RY, WS). Carbon County: Fort Steele, August 19, 1901, *Goodding* 543 (C, CO, G, RY). Sublette County: Newfork Lakes, July 20, 1925, *Payson & Payson* 4835 (G, PA, RY, WS). STATE UNDETERMINED. Rocky Mountains, Lewis's River, *Nuttall* (type of *A. denudatus* Nutt.) (G, PA); Rocky Mountains, Lewis's River, *Nuttall* (type of *A. ramulosus* Nutt.) (PA).

7b2. *Aster chilensis* Nees subsp. *adscendens* (Lindl. ex DC.) Cronquist
var. *bernardinus* (Hall) Cronquist comb. nov.

Aster bernardinus Hall U. Cal. Pub. Bot. 3:79. 1907.

Aster Menziesii Lindl. ex DC. var. *bernardinus* Jeps. Man. Pl. Calif. 1046. 1925.

Plant densely pubescent with spreading mostly straight hairs; leaves linear or narrowly lanceolate. Waste places; southern California.

Type: Parish 5543, September 5, 1905, vicinity of San Bernardino, San Bernardino County, California, in University of California Herbarium.

This is a troublesome variety which closely approaches more pubescent forms of *A. commutatus* T. & G. var. *crassulus* (Rydb.) Blake, and may yet prove to be more closely allied to *A. commutatus* than to *A. chilensis*. Inasmuch as it occurs in the range of subsp. *adscendens*, and usually has the acuminate inner phyllaries of that subspecies, it has been placed there as a local variety.

SPECIMENS SEEN: CALIFORNIA. Los Angeles County: experiment station near Pomona, October 19, 1896, Davy 2870 (C). Orange County: Anaheim marsh, September 8, 1933, Booth 1392 (C, PO). San Bernardino County: San Bernardino valley, September, 1880, Parish 573 (C, G, PA); vicinity of San Bernardino, September 5, 1908, Parish 5543 (type of *A. bernardinus* Hall) (C, G, PO, RY). San Diego County: vicinity of San Diego, Wright 73 (C).

7c. *Aster chilensis* Nees subsp. *Hallii* (Gray) Cronquist comb. nov.

Aster Hallii Gray Proc. Am. Acad. 8: 368, 1872, as a nomen nudum.

Aster Hallii Gray Syn. Fl. 1(2):191. 1884.

Aster mucronatus Sheld. Bull. Torrey Club 30:309. 1903.

Leaves mostly glabrous or nearly so except for the commonly scabrous margins and tips, linear, mostly less than 6 cm. long and 5 mm. wide, neither narrowed nor enlarged at the bases, not at all auriculate; inflorescence conspicuously bracteate, the bracts mostly less than 1 cm. long, $\frac{1}{4}$ - $\frac{1}{2}$ as wide, obtuse or acutish; heads small, the disks 5-8 mm. high and 6-9 mm. wide; innermost phyllaries obtuse or acute; ligules white or sometimes bluish. Dry or less frequently moist ground in the valleys and plains; Oregon, chiefly west of the summit of the Cascade Mountains, occasionally in Washington.

Type: Henderson 14, 1883, Hood River, Hood River County, Oregon, in Gray Herbarium.

The three forms which I have treated as subspecies of *A. chilensis* pass imperceptibly into each other where their ranges meet. Occasional specimens from well within the range of one form or another are referable only by virtue of where they were collected, being intermediate in appearance or partially simulating one of the other subspecies.

SPECIMENS SEEN: OREGON. Clackamas County: Eagle Creek, September 23, 1925, Suksdorf 3372 (C, G, WS). Douglas County: Winchester, Umpqua valley, August 21, 1914, Cusick 4471 (WS). Hood River County: Hood River, 1883, Henderson 14 (type of *A. Hallii* Gray) (G); Odell, August 24, 1927, Suksdorf 3392 (C, G, WS). Jackson County: between Ashland and foot of Siskiyou grade, September 7, 1927, Abrams 12104 (RY). Multnomah County: Mount Scott, August 15, 1902, Sheldon 11172 (type of *A. mucronatus* Sheld.) (G, NY, US, WS). County undetermined: banks of Snake River, September 27, 1898, Cusick 2122 (WS). WASHINGTON. King County: Seattle, September 19, 1931, Thompson 8107 (C). Okanogan County: Conconully, September 1, 1932, Fiker 1151 (WS). Yakima County: Yakima region, September, 1883, Brandegee 860 (G).

8. *ASTER OCCIDENTALIS* (Nutt.) T. & G. Fl. N. Am. 2:164. 1841.

Stems 2-10 dm. high, commonly arising singly or two or three together from slender rhizomes, mostly red or brownish, usually rather scantily pubescent, the pubescence uniform under the heads but often in lines below, occasionally the whole herbage densely and closely pubescent; leaves commonly glabrous

and entire, linear to lanceolate or oblong, the lower frequently oblanceolate and tapering to winged petioles or petioliform bases, the blade and petiole, if present, 4-15 cm. long and 5-20 mm. wide, sometimes deciduous; middle stem leaves 3-12 mm. wide, 3-15 cm. long, mostly 7-20 times as long as broad; upper leaves more or less reduced, particularly in large plants; heads 1-many, usually in a broad open cymose panicle and the leaves of the inflorescence reduced and bract-like; heads small to medium-sized, the disks mostly 6-10 mm. high and 8-15 mm. broad; phyllaries loose or appressed, occasionally somewhat spreading, obtuse or more commonly acute, linear or oblong, slightly if at all narrowed at the bases, often purple-tipped but seldom purple-margined, usually glabrous on the backs but frequently pubescent within, the margins often ciliate, scarious margins narrow or wanting; outer phyllaries as long as the inner or decidedly shorter, wholly green, or white-margined at the bases; ligules 6-15 mm. long, rose purple or more commonly blue to violet; achenes pubescent; pappus white or somewhat tawny, not reddish. Meadows, streambanks, and hillsides; Washington to California, east to Montana, Wyoming, and Colorado, and apparently northward in Canada to Bear Lake.

Type: Lewis, by muddy streams, Rocky Mountains, in Philadelphia Academy of Science Herbarium; isotype in Gray Herbarium.

KEY TO THE VARIETIES

1. Plant very leafy, the leaves linear, the internodes less than 2 cm. longc. var. *yosemitanus*
1. Plant less conspicuously leafy, the leaves linear to oblanceolate or oblong; internodes over 2 cm. long.
 2. Heads many; lower leaves mostly over 10 cm. long, often deciduous; upper leaves many, reduced and bract-likeb. var. *intermedius*
 2. Heads usually few; lower leaves less than 10 cm. long, persistent; upper leaves fewer, usually not so conspicuously reduced.a. var. *typicus*

8a. *Aster occidentalis* (Nutt.) T. & G. var. *typicus* Cronquist nom. nov.

Aster spathulatus Lindl. ex DC. Prodrum 5:231. 1836.

Not *Aster spathulatus* Lag. ex Nees Aster 283. 1832.

Tripolium occidentale Nutt. Trans. Am. Phil. Soc. n. ser. 7:296. 1840.

Aster andinus Nutt. Trans. Am. Phil. Soc. n. ser. 7:290. 1840.

Aster occidentalis T. & G. Fl. N. Am. 2:164. 1841.

Aster adscendens Lindl. ex DC. var. *Fremonti* T. & G. Fl. N. Am. 2:503. 1841.

Aster Fremonti Gray Syn. Fl. 1(2):191. 1884.

Aster Fremonti (T. & G.) Gray var. *Parishii* Gray Syn. Fl. 1(2):192. 1884.

Aster subspathulatus Rydb. Mem. N. Y. Bot. Gard. 1:395. 1900.

? *Aster armeriaefolius* Greene Pitt. 4:214. 1900.

? *Aster corymbiformis* Rydb. Bull. Torrey Club 31:655. 1904.

Aster delectabilis Hall. U. Cal. Pub. Bot. 3:82. 1907.

? *Aster adscendens* Lindl. ex DC. var. *armeriaefolius* A. Nels. N. Man. Rocky Mt. Bot. 517. 1909.

Aster Williamsii Rydb. Bull. Torrey Club 37:136. 1910.

Aster delectatus Piper Contr. U. S. Nat. Herb. 16:210. 1913.

Aster adscendens Lindl. ex DC. var. *delectabilis* Jeps. Man. Pl. Calif. 1047. 1925.

Mostly less than 5 dm. high; lower leaves mostly less than 10 cm. long, usually persistent; heads mostly over 1 cm. broad, comparatively few, mostly less than 10, in a simple nearly naked cyme or cymose panicle. Meadows;

mountains of Washington to California, east to Colorado and Wyoming, and apparently far northward into Canada.

Type: Lewis, by muddy streams, Rocky Mountains, in Philadelphia Academy of Science Herbarium; isotype in Gray Herbarium.

PLATE 15



Type of *Aster Fremonti* (T. & G.)
Gray var. *Parishii* Gray (= *A. occidentalis*
var. *typicus*).

Isotype of *Aster spathulatus* Lindl. ex
DC. (= *A. occidentalis* var. *typicus*).

Aster Fremonti (T. & G.) Gray cannot be separated even varietally from *A. occidentalis* var. *typicus*. The two forms grow in exactly the same habitats, and none of the characters supposed to distinguish them from each other shows any degree of constancy.

SPECIMENS SEEN: BRITISH COLUMBIA. Lake O'Hara, August 9, 1904, Macoun (G). NORTHWEST TERRITORY. Bear Lake, Richardson (type of *A. spathulatus* Lindl.) (G). CALIFORNIA. Butte County: Jonesville, August 4, 1930, Copeland 485 (CO, PO). Eldorado County: Benwood meadow, September 10, 1915, Heller 12259 (CO, PA).

Mariposa County: Lake Tenaya trail, August 14, 1894, *Congdon* 135 (C, G). Nevada County: above Donner Lake, August 7, 1903, *Heller* 7115 (C, G, PA, RY); lower end of Donner Lake, August 11, 1903, *Heller* 7146 (C, G, PO, RY). San Bernardino County: Cienega, between Bear valley and Bluff Lake, July 30, 1902, *Abrams* 2812 (C, G, PO); Bluff Lake, July 9, 1931, *Clokey* 5316 (C, UT, WS); Big Meadows, Santa Ana River, August 21, 1922, *Munz* 6800 (C, G, PO); Bear Valley, San Bernardino Mountains, August, 1882, *Parish & Parish* 180 (type of *A. Fremonti* var. *Parishii* Gray) (G); Mill Creek, San Bernardino Mountains, August 30, 1904, *Smith* 76 (type of *A. delectabilis* Hall) (C). Tulare County: Kaweah Meadows, April-September, 1897, *Purpus* 5162 (C, G). COLORADO. Boulder County: Lake Eldora, August 16, 1918, *Clokey* 3211 (C, G, RY). Grand County: Shippler Park, August 15, 1921, *Clokey* 4346 (C, PO, RY, WS). Lake County: Twin Lakes, July 19, 1919, *Clokey* 3445 (G, PO, RY, WS). Saguache County: Marshall Pass, July 19, 1901, *Baker* 519 (G, PO, RY). IDAHO. Boise County: Pinehurst, August 17, 1911, *Macbride* 1680 (C, PO, WS). Bonner County: near Weeksville, August 22, 1895, *Leiberg* 1569 (C, PO, RY). Camas County: Camas Prairie, Corral, August 15, 1916, *Macbride & Payson* 3838 (C, G, PO, RY). Clark County: Sheridan Creek, July 31, 1937, *Cronquist* 778B (CR). Fremont County: Elk Creek, July 27, 1939, *Cronquist* 1804 (UT). MONTANA. Sanders County: Paradise, September 17, 1927, *Kirkwood* 2509 (G, RY); Thompson's Falls, August 28, 1892, *Sandberg, MacDougall & Heller* 980 (C, PO). NEVADA. Elko County: Deeth, July 17, 1908, *Heller* 9030 (C). Lander County: Bunker Hill Canyon, July 29, 1913, *Kennedy* 4168 (C). White Pine County: Mount Jeff Davis, August 26, 1933, *Maguire & Richards* 2833 (CO, UT). OREGON. Crook County: Beaver Marsh, September 1, 1902, *Cusick* 3004, (CO, PO, WS). Klamath County: Cyeon Marsh, August 12, 1901, *Cusick* 2746 (C, CO, G, PO, RY, WS); Cyeon River, August 15, 1901, *Cusick* 2761 (type of *A. delectus* Piper) (C, CO, G, PO); Deschutes River at Odell, September 2, 1902, *Cusick* 3005 (C, CO, G, PO, WS); near Crater Lake, August 19, 1902, *Cusick* 3007 (C, CO, G, PO). Lane County: Fall Creek into Willamette River, August 2, 1931, *Henderson* 14067 (C). Wallowa County: Imaha River, August 18, 1909, *Cusick* 3390 (G, RY, WS). UTAH. Cache County: Tony Grove Lake, August 5, 1938, *Maguire* 16092 (UT). Iron County: Midway Creek Camp, August 15, 1937, *Gierisch* 535 (CR, UT). Sevier County: Fish Lake, August 10, 1894, *Jones* 5758 (C, PO, RY); Fish Lake, August 11, 1934, *Maguire & Richards* 15723 (CO, RY, UT). Washington County: Pine Valley Mountains, August 1, 1934, *Maguire & Richards* 15018 (UT). WASHINGTON. Chelan County: Peshastin, August 25, 1893, *Sandberg & Leiberg* 807 (C, G, WS). Pierce County: Mount Rainier, August 24, 1937, *Jones* 10489 (G). Skamania County: August 20, 1892, *Suksdorf* 2169 (G, WS). WYOMING. Albany County: Nash's Fork, July 28, 1900, *Nelson* 7772 (C, CO, G, RY). Big Horn County: Bill's Flat, July 25, 1901, *Goodding* 349 (C, PO, RY). Johnson or Sheridan County: North Fork of Clear Creek, August 12, 1898, *Williams* (type of *A. Williamsii* Rydb.) (NY). Teton County: String Lake, August 15, 1937, *Cronquist* 838 (CR, UIS, UT). Washakie County: Baby Wagon Creek, July 9, 1936, *Williams & Williams* 3298 (G, RY, WS). STATE UNDETERMINED: Rocky Mountains, by muddy streams, *Lewis* (type of *Tripolium occidentale* Nutt.) (G, PA).

8b. *ASTER OCCIDENTALIS* (Nutt.) T. & G. var. *INTERMEDIUS* Gray

Syn. Fl. 12:192. 1884.

Mostly over 5 dm. high; lower leaves enlarged, tapering to winged petioles, the blade and petiole together mostly 10-15 cm. long, often deciduous; middle and upper leaves conspicuously reduced, rather numerous, and bract-like; heads comparatively many in an open cymose panicle and comparatively small, the disks seldom much over 1 cm. broad. Meadows, streambanks, and hillsides; Washington and adjacent Idaho to central California, mostly east of the Cascade and Sierra Nevada summits.

PLATE 16



Type of *Aster occidentalis* (Nutt.) T.
& G. var. *intermedius* Gray.

Type of *Aster delectabilis* Hall (= *A.*
occidentalis var. *typicus*).

Type: Suksdorf 62, Falcon valley, Klickitat County, Washington, September 5, 1882, in Gray Herbarium.

SPECIMENS SEEN: CALIFORNIA. Madera County: Soda Springs, upper San Joaquin, August 20, 1895, Congdon (G). Placer County: Summit valley, September 22, 1882, Pringle (cotype of *A. adscendens* var. *yosemitanus* Gray) (G). Siskiyou County: near Edgewood, Butler 1880 (C). NEVADA. Washoe County: Incline, July 25, 1907, Brown (C). OREGON. Hood River County: near Odell, August 25, 1919, Suksdorf 2118 (C, G, WS). Klamath County: Dead Indian, August 14, 1902, Cusick 2952 (C, CO, G, PO, WS); along Crescent Creek, August 17, 1934, Constance 976 (C, CO, G, PO, RY, WS); near Crater Lake, August 28, 1902, Cusick 2988 (C, CO, G, PO, WS). Umatilla County: Bingham Springs, October 10, 1908, Cusick 3327 (C, G, WS). WASHINGTON. Klickitat County: 1.5 miles west of White Salmon, August 26, 1927, Keck 313 (C, PO); Falcon Valley, September 5, 1882, Suksdorf 62 (357) (type of *A. occidentalis* var. *intermedius* Gray) (C, G). Okanogan County: northwest of Omak, July 20, 1934, Ficker 1583 (WS). Whitman County: Pullman, August 12, 1893, Piper 1695 (G, WS).

8c. *Aster occidentalis* (Nutt.) T. & G. var. *yosemitanus* (Gray)

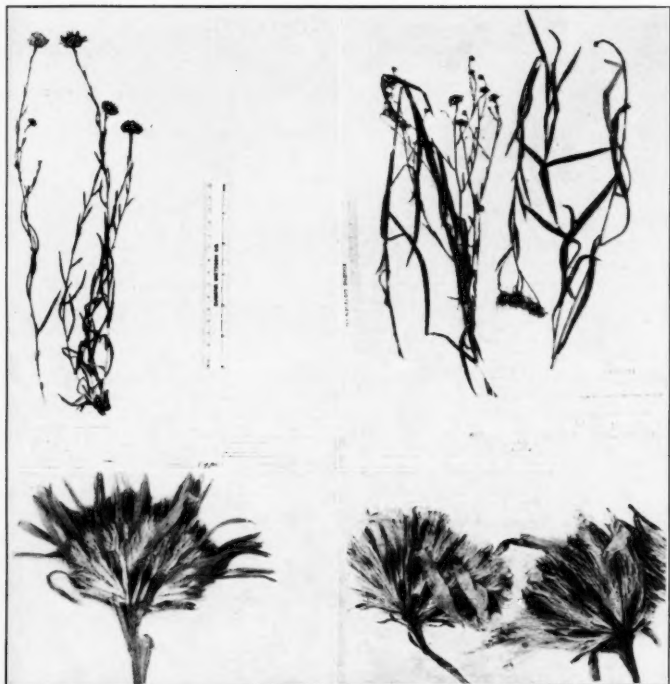
Cronquist comb. nov.

Aster adscendens Lindl. ex DC. var. *yosemitanus* Gray Syn. Fl. 1(2):191. 1884.*Aster yosemitanus* Greene Fl. Francisc. 383. 1897.*Aster Copelandi* Greene Leaflet 1:200. 1906.*Aster paludicola* Piper Contr. U. S. Nat. Herb. 16:210. 1913.

Leaves mostly linear, the lower not broader than the middle and upper; internodes short, mostly less than 2 cm. long; heads few or rather many. Meadows and streambanks; southern Oregon to southern California.

Type: Hooker & Gray, 1877, near Vernal Fall, Yosemite National Park, in Gray Herbarium.

PLATE 17



Type of *Aster adscendens* Lindl. ex DC. var. *yosemitanus* Gray (= *A. occidentalis* var. *yosemitanus*).

Type of *Aster paludicola* Piper (= *A. occidentalis* var. *yosemitanus*).

Aster occidentalis var. *yosemitanus* is of rather sporadic occurrence, and is distinguishable only with difficulty from the typical form of the species.

SPECIMENS SEEN: CALIFORNIA. Eldorado County: Cascade Lake, July 25, 1910, Hall 8812 (C, G). Riverside County: San Jacinto Mountains, Strawberry valley, Hall 2625 (C). Siskiyou County: Mount Eddy, September 7, 1903, Copeland 3867 (type of *A. Copelandi* Greene) (C, G, PO, WS). Tulare County: Kern Canyon, July, 1904, Hall & Babcock 5567 (C). Yosemite National Park: near Vernal Fall, 1877, Hooker & Gray (type of *A. adscendens* var. *yosemitanus* Gray) (G). NEVADA. Elko County: Mountain City, August 9, 1912, Nelson & Macbride 2183 (G, RY) (probably belongs here). OREGON. Josephine County: Eight Dollar Mountain, August 15, 1907, Piper (type of *A. paludicola* Piper) (US).

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New Vascular Plants from Texas, Mexico, and Central America

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(and Collaborators)

In the present paper one new genus, *Maléa* of the Ericaceae, 32 new species, and three transfers are included along with critical notes on various other plants. Among the new species are four from Texas in the genera *Eleocharis*, *Linum*, *Forestiera*, and *Tetraclea*. The new species from Mexico and Central America belong to *Merostachys*, a grass genus not recorded previously from North America, *Scleria*, *Roupala*, *Phoebe*, *Crotalaria*, *Erythroxylon*, *Amanoa*, *Euphorbia*, *Sapium*, *Hypericum*, *Calyptanthus*, *Eugenia*, *Myrcia*, *Psidium*, *Tibouchina*, *Maléa*, *Ardisia*, *Cordia*, *Solanum*, *Russelia*, and *Chiococca*. Transfers are made in the genera *Neea*, *Thamnosma*, and *Sapium*. The writer is indebted to Mr. Jason R. Swallen, Dr. Henry K. Svenson, and Dr. Leon Croizat for the descriptions of five of the novelties included herein.

Merostachys pauciflorus Swallen, sp. nov.

Fig. 1.

Culmi alti, tubulati, usque ad 3.5 cm. crassi, retrorse scabri vel sparse hirsuti; rami dense fasciculati usque ad 40 cm. longi, glabri, internodiis intermediis elongatis, superioribus et inferioribus abbreviatis, rami floriferi saepe breves efoliati; vaginae omnes glabrae, inferiores ramorum foliosorum efoliatae, in ore fimbriatae. Laminae lanceolatae, acuminatae, 7-12 cm. longae, 8-14 mm. latae, petiolo 2-3 mm. longo. Racemus 3-5 cm. longus, (1)-3-8 spiculatus, rache dense pubescenti. Spiculae inflatae, 10-12 mm. longae, adscendentes vel reflexae, pedicello pubescenti 2 mm. longo. Glumae subaequales, 7-nerviae quam spicula paulo breviores; gluma prima late-lanceolata, acuta; gluma secunda oblonga abrupte acuta vel apiculata, marginibus prope apicem ciliatis. Lemma glumam secundam simulans, firmum, glabrum, lucidum obscure \pm 15-nervium. Palea lemmate paulo longior carinis approximatis. Rachilla producta, villosa inter carinas palearum occulta.



Fig. 1. *Merostachys pauciflorus* Swallen. Type, Gentle 3485, in the herbarium of the U.S. National Arboretum. Inflorescence, natural size; florets, two and one-half times natural size.

Culms tall, slender, hollow, as much as 3.5 cm. thick at the base, retrorsely scabrous and sometimes appressed hirsute especially above the nodes; leafy branches very slender, smooth, numerous in dense whorls from just above the nodes, as much as 40 cm. long, with short leafless flowering branches intermixed, the leafy branches often bearing inflorescences, these whorls, then, usually without shorter leafless flowering branches; lower internodes of the branches short, the middle ones elongate with short leafless sheaths, the several upper ones again short with overlapping leaf-bearing sheaths; sheaths glabrous, fimbriate at the mouth. Blades rather thin, shiny, lanceolate, acuminate, 7 to 12 cm. long, 8 to 14 mm. wide, rounded and narrowed at the base to a short petiole 2 to 3 mm. long. Inflorescence a simple raceme, the 3-sided axis densely pubescent bearing 3 to 8 spikelets or sometimes reduced to a single spikelet. Spikelets inflated, 10 to 12 mm. long, solitary, distant, alternate on two sides of the rachis, ascending to finally reflexed, the densely pubescent pedicels about 2 mm. long. Glumes subequal, glabrous, 7-nerved, a little shorter than the spikelet, the first broadly lanceolate, acute, the second oblong, abruptly narrowed at the somewhat saccate tip to a short point, the margins ciliate toward the summit. Lemma about as long as the second glume and similar to it in shape, firm, smooth and shining, about 15-nerved, the nerves obscure. Palea a little longer than the lemma, similar in texture, the keels close together, enclosing between them the prolonged rachilla; rachilla villous in the upper half, the hairs protruding from between the keels of the palea.

BRITISH HONDURAS: Stann Creek District, Stann Creek Valley, on bank of Big Eddy Creek, January 12, 1941, Percy H. Gentle 3485 (type in the herbarium of the U. S. National Arboretum, No. 145,106; duplicate in the University of Michigan Herbarium).

M. pauciflorus is the first species of this genus to be found in North America. In the South American species the spikelets are crowded, numerous, and pectinately arranged on the rachis. These characters are in striking contrast to the few-flowered racemes of large, inflated, spreading or reflexed, relatively distant spikelets of the species described above.

Eleocharis Lundellii Svenson, sp. nov.

Fig. 2

Annua, cespitosa, culmis capillaribus tenuibus, 10-17 cm. altis, quadrangulato-sulcatis, glauco-viridibus; spicis lanceolato-ovatis, 3-4 mm. longis, subacutis, multifloris, squama (vel bractea) infima, subulato-viride, spicam subaequant; glumis obtusis, 1-1.5 mm. longis, obscure carinatis, margine late hyalinis, latere castaneo-purpureis; staminibus 2; stylo 3-fido; acheniis obtuse trigonis, obovatis, 0.5-0.6 mm. longis, margaritaceo-albidis, immaturis viridibus, subtilissime nigro-punctulato; stylo-basi conico-depresso, apiculato; setis nullis.

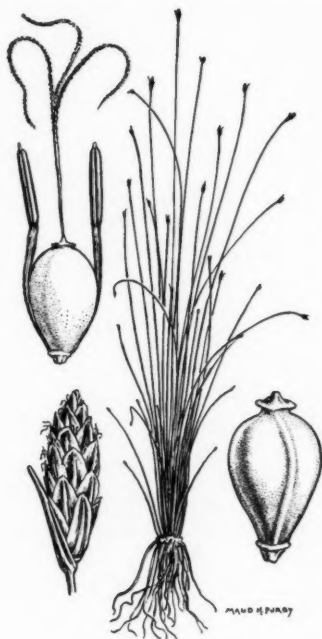
Cespitose annual, culms capillary, 10 to 17 cm. high, quadrangular-sulcate. Spikelets lanceolate-ovate, 3 to 4 mm. long, subacute, many-flowered, with a conspicuous subulate basal bract. Scales obtuse, 1 to 1.5 mm. long, obscurely carinate, margin broadly hyaline. Stamens 2. Style 3-fid. Achene obtusely

trigonus, obovate, 0.5 to 0.6 mm. long. Style depressed conic at base, apiculate. Bristles none.

TEXAS: Hardin County, southwest of Kountze, in marshy pine land, April 14, 1942, C. L. Lundell and Amelia A. Lundell 11157 (type in the University of Michigan Herbarium, duplicate in the herbarium of the Brooklyn Botanic Garden).

This little species is most closely related to *E. microcarpa* var. *Brittonii* from which it differs in smaller size and in the presence of a conspicuous green bract at the base of the spikelet—a character not otherwise associated with the genus *Eleocharis*. The style-base is elevated on a slight constriction at the apex of the achene.

Fig. 2. *Eleocharis Lundellii* Svenson. Type, Lundell and Lundell 11157, in the University of Michigan Herbarium. Habit, half natural size; spikelet, five times natural size; flower and achene, fifty times natural size.



Scleria areolata Lundell, sp. nov.

Annua, ad 35 cm. alta; culmis gracilibus. Folia 8-27 cm. longa, 1-2.5 mm. lata, glabra, vaginis breviter pilosis. Inflorescentia paniculata, ad 15 cm. longa, glomerato-spicata; ramis paucis, remotis; bracteis lineari-setaceis; spiculis ca. 3 mm. longis, remotis; squamis ovato-lanceolatis, acuminatis; hypogynio nullo; achaenio trigono-globoso, 1 mm. longo, inconspicue areolato, apiculato, ad basin trigono, poroso.

Annual, up to 35 cm. high, roots fibrous. Culms slender, triquetrous. Leaves 8 to 27 cm. long, 1 to 2.5 mm. wide, glabrous, sometimes sparsely scabrous on the margins and nerves, usually exceeding the culms; sheaths reddish, short pilose; ligule inconspicuous, pilose. Inflorescence paniculate, lax, up to 15 cm. long, the branches very slender, up to 5 cm. long; rachis triquetrous, the angles pilose; fascicles small, distant; bracts setaceous, inconspicuous. Spikelets about 3 mm. long; scales ovate-lanceolate, acuminate, inconspicuously scabrous on the keel. Hypogynium none. Achene trigono-globose, 1 mm. long, white, shining, areolate, apiculate, the base trigonous, about 0.2 mm. long, 4- or 5-porose on each face.

BRITISH HONDURAS: Toledo District, Swasey Branch, Monkey River, in high ridge, July 7, 1942, *Percy H. Gentle 4047* (type in the University of Michigan Herbarium); near Jenkins Creek, north of Monkey River, in wet area in pine ridge, Sept. 28, 1942, *Gentle 4193, 4194*.

Scleria areolata, referable to the section *Hypoporum*, has affinity to *S. micrococca* (Liebm.) Steud. The British Honduran plant differs in having inconspicuously areolate achenes with 4 or 5 pores on each face of the trigonous base and elongate leaves exceeding the culms and fully twice as long as in *S. micrococca*.

SCIRPUS SUPINUS L., Sp. Pl., 49. 1753.

TEXAS: Kenedy County, Kings Ranch, near Norias, on sand in low area, March 15, 1942, *C. L. Lundell and Amelia A. Lundell 10745*.

Dr. H. K. Svenson, who identified the species, comments as follows. "This plant has trigonous achenes and a 3-cleft style, just as in typical European material. It has not been reported from the United States since the time of Asa Gray, Man. ed 5: 'In Texas occurs the normal *S. supinus*, with 3-cleft style and triangular achenium, as in Europe. . . .' The plant which has been called *S. Hallii* A. Gray has, in my estimation, achenes identical with those in specimens from France and Australia, and I can see no reason for treating it other than a variety of *S. supinus* with 2-cleft style and lenticular (often almost trigonous) achene. *S. supinus* has an erratic distribution similar to that of *Eleocharis atropurpurea* (Retz) Kunth."

Roupala repanda Lundell, sp. nov.

Arbor parva, ramulis crassis, angulatis, parce rufo-pubescentibus. Folia longe petiolata, petiolo 3-6.5 cm. longo, lamina coriacea, glabra, pallida, late ovata, 8-14 cm. longa, 4.5-8.5 cm. lata, apice subabrupte longe acuminata, basi rotundata et abrupte acuta, margine repanda vel crenato-repanda. Inflorescentiae axillares, racemosae, ad 17 cm. longae. Pedicelli fructiferi crassi, ad 3 mm. longi. Folliculi 4 cm. longi.

Small tree, 5 cm. in diameter; branchlets stout, angled, sparsely pubescent with reddish hairs; buds densely pubescent with reddish hairs. Petioles canaliculate, 3 to 6.5 cm. long, densely pubescent at base on upper side. Leaf blades coriaceous, rigidly so at maturity, glabrous, pallid, concolorous, broadly ovate, 8 to 14 cm. long, 4.5 to 8.5 cm. wide, apex subabruptly long acuminate, base rounded and abruptly decurrent, margin repand or crenate-repand almost to base, costa and veins subimpressed above, prominent beneath, primary veins 6 or 7 on each side, branching and anastomosing about half way to margin, veinlets obscure. Racemes axillary, in fruit short sericeous, up to 17 cm. long, recurved. Fruiting pedicels stout, up to 3 mm. long. Follicles 4 cm. long, oblong-elliptic, compressed, stipitate, with persistent style; stipe thick, about 5 mm. long; body about 3.5 cm. long, 1.3 cm. wide.

BRITISH HONDURAS: Toledo District, Monkey River, in hammock in pine ridge near Jenkins Creek, Sept. 28, 1942, *Percy H. Gentle 4196* (type in the University of Michigan Herbarium), tree, 2 inches in diameter.

The species, apparently closely related to *R. panamensis* Pittier, is remarkable for its large thick broadly ovate repand leaves, long petioles, and axillary racemes up to 17 cm. long.

Neea choriophylla Standl. var. *hirtella* (Lundell) Lundell, comb. nov.

Neea hirtella Lundell, Bull. Torrey Bot. Club 69:388. 1942.

This appears to be only a pubescent variety. Typical *N. choriophylla* is entirely glabrous.

Phoebe mayana Lundell, sp. nov.

Arbor, ramulis crassiusculis, adpresse puberulis. Folia petiolata, petiolo 6-15 mm. longo, lamina chartacea, oblongo-oblancoolata, 6.5-14.5 cm. longa, 2.1-4.5 cm. lata, apice obtusa, basi attenuata. Inflorescentiae paniculatae, ad 13 cm. longae. Cupula parva. Bacca oblonga, usque ad 1.5 cm. longa, 7 mm. diam.

A tree, 30 cm. in diameter; branchlets stout, angled, appressed puberulent, the indument at first dense. Petioles canaliculate, appressed puberulent, 6 to 15 mm. long. Leaf blades chartaceous, oblong-oblancoolate, 6.5 to 14.5 cm. long, 2.1 to 4.5 cm. wide, apex obtuse or subabruptly acuminate, the acumen bluntly obtuse, base attenuate, decurrent, minutely sericeous on undersurface, sericeous along costa and veins above, glabrescent with age, domatia in the axils of the primary veins, costa and veins slightly raised on both surfaces, conspicuous, primary veins 8 to 10 on each side. Inflorescence axillary, paniculate, up to 13 cm. long, with minute appressed indument which disappears with age. Flowers unknown. Fruiting pedicels thickened to base, up to 8 mm. long, 4.2 mm. in diameter above. Cupule very shallow, up to 5 mm. in diameter, the tepals deciduous. Fruits oblong, up to 1.5 cm. long, 5 to 7 mm. in diameter, abruptly rounded at apex and base.

BRITISH HONDURAS: Stann Creek District, Baboon Ridge, Stann Creek Valley, in high ridge on top of hill, Feb. 2, 1940, Percy H. Gentle 3187 (type in the University of Michigan Herbarium), bark whitish, wood white, vernacular name, *timber sweet*.

Crotalaria belizensis Lundell, sp. nov.

Herba annua ad 30 cm. alta, dense hirsuta. Folia breviter petiolata, anguste linearia, 1-6 cm. longa, 1.5-3 mm. lata, apice acuta, basi obtusiuscula. Inflorescentiae 1- vel 2-florae, ad 5 cm. longae; calyce ca. 1 cm. longo, hirsuto, profunde lobato, lobis lanceolatis, attenuatis. Corolla flavida. Legumen oblongum, ad 2.5 cm. longum, ca. 8 mm. latum, glabrum.

Erect annual up to 30 cm. high, usually with few spreading branches near the base, conspicuously hirsute with spreading hairs. Stipules rarely present, decurrent on the stem, attenuate at apex. Leaves simple, hirsute, subsessile, the petioles less than 2 mm. long. Leaf blades uniformly linear, 1 to 6 cm. long, 1.5 to 3 mm. wide, apex acute, base obtusish, costa impressed above, elevated beneath. Inflorescence lateral, 1- or 2-flowered, up to 5 cm. long, the peduncle and pedicels hirsute; bracts and bractlets linear-lanceolate. Bractlets at base of calyx 2, about 5 mm. long. Calyx about 1 cm. long, hirsute, deeply lobed, the

lobes narrowly lanceolate, attenuate to the apex, the tube short. Corolla yellow, about a fourth shorter than the calyx. Legume oblong, up to 2.5 cm. long, about 8 mm. in diameter, glabrous, apiculate.

BRITISH HONDURAS: Toledo District, north of Monkey River in pine ridge near Jenkins Creek, Sept. 11, 1942, Percy H. Gentle 4144 (type in the University of Michigan Herbarium), flowers yellow.

C. belizensis belongs to the complex of *C. sagittalis* L., and like other members of the group, differs only in minor characteristics from related forms. The species is noteworthy for its annual habit, very narrow uniformly linear leaves, dense spreading pubescence, development of stipules (when present) only on the upper third of the stem, and 1- or 2-flowered inflorescences.

Erythroxylon multiflorum Lundell, sp. nov.

Arbor parva, glabra. Stipulae striatae, lanceolato-subulatae, 4-8 cm. longae. Folia magna, petiolata, petiolo 1-1.5 cm. longo, lamina coriacea, oblongo-elliptica, 11-30 cm. longa, 4-10 cm. lata, apice acuminata, basi acuta, nervis lateralibus utroque latere 12-19. Flores axillares, fasciculati, dense congesti, numerosi, pedicellis angulatis, 6-11 mm. longis. Calyx ca. 5.5 mm. longus, lobis ovatis, acuminatis. Petala oblonga, 4.5-5 mm. longa.

Small glabrous tree, about 7 m. high, 12.5 cm. in diameter; branchlets thick, terete, bearing conspicuous stipular scars. Stipules imbricate, dark brown, striate, lanceolate-subulate, usually 4 to 8 cm. long, persistent. Petioles stout, canaliculate, 1 to 1.5 cm. long. Leaf blades coriaceous, glabrous, paler beneath, oblong-elliptic, 11 to 30 cm. long, 4 to 10 cm. wide, apex acuminate, base acute and decurrent, primary veins 12 to 19 on each side, conspicuous but not prominent, venation finely reticulate. Fascicles dense, many-flowered. Pedicels 6 to 11 mm. long, angulate. Calyx deeply cleft, the lobes broadly ovate, 5 mm. long, acuminate. Petals oblong, 4.5 to 5 mm. long, the ligule-lobes conspicuous. Stamen tube about 1.8 mm. long. Ovary glabrous.

PANAMA CANAL ZONE: vicinity of Juan Mina, on hill at Canal Zone boundary, July 27, 1940, H. H. Bartlett and T. Lasser 16566 (type in the University of Michigan Herbarium), tree, 5 inches in diameter, 20 feet tall, sepals green, petals whitish. REPUBLIC OF PANAMA: Province of Panama, vicinity of Rio Pescado, at southeastern part of Gatun Lake, July 30, 1940, Bartlett and Lasser 16596, tree, 20 feet tall.

E. multiflorum, of the section Macrocalyx, bears a close resemblance to *E. Skutchii* Standl. of Costa Rica. The latter has much coarser venation, fewer primary veins, shorter pedicels, smaller flowers, and stipules deciduous early.

Linum spinescens Lundell, sp. nov.

Annua, usque ad 35 cm. alta, glabra. Folia sessilia, linearia, 1-2.5 cm. longa, ad 2.5 mm. lata, apice attenuata, spinulosa, uninervia. Cymae pauciflorae. Sepala lanceolata vel ovato-lanceolata, 5.5-7 mm. longa, glanduloso-dentata, aristata, unicostata. Petala cuneato-obovata, 11-14 mm. longa. Capsula ovoidea, 4.5-5 mm. longa.

Annual, up to 35 cm. high, glabrous. Stems branched at the base, the branches stout, ascending, striate or striate-angled, sparingly corymbose-branched above, the branches of the inflorescence rather short and stout, the cymes few-flowered. Stipules minute, red-glandular. Leaves erect or appressed, alternate, sessile, linear, 1 to 2.5 cm. long, up to 2.5 mm. wide, usually less than 1.5 mm. wide, the basal smaller, apex attenuate and spinescent, strongly 1-nerved, the lateral veins inconspicuous at base, the margin minutely scabridulous at apex, entire, usually revolute. Bracts lanceolate, spinescent, the margin toothed and often glandular. Sepals lanceolate or ovate-lanceolate, 5.5 to 7 mm. long, rarely up to 9 mm. long, subequal or the inner shorter, the margin wide and coarsely toothed, the teeth gland-tipped, apex attenuate and conspicuously awned, the awn up to 2 mm. long, the midvein crested and erose, the lateral veins inconspicuous. Petals yellow or orange-yellow, with a reddish eye at base, barbate inside slightly above base, cuneate-obovate, 11 to 14 mm. long. Stamens glabrous; staminodia none. Ovary glabrous. Styles united, free at apex only, glabrous, up to 8 mm. long. Capsules ovoid, 4.5 to 5 mm. long, with very conspicuous cartilaginous thickenings at base.

TEXAS: Brooks County, north of Encino, in live-oak belt, along sandy roadside, May 10, 1940, C. L. Lundell and Amelia A. Lundell 8848 (type in the University of Michigan Herbarium, duplicate in the herbarium of Southern Methodist University). Cameron County, near Boca Chica, on top of sand dune, May 1, 1940, Lundell and Lundell 8605.

The sepals of *L. spinescens* have the broad coarsely glandular-toothed margin of *L. alatum* (Small) H. Winkl. and the awns of *L. aristatum* Engelm. The species is noteworthy further for its stout branches, 1-nerved aristate leaves, small sepals with crested midvein, and petals barbate on inside at base. All of the species referred by Small to the genus *Cathartolimum*, section *Rigida* N. Am. Fl. 25:69. 1907) are closely related, and will need reinterpretation as soon as adequate collections become available.

Thamnosma texanum (A. Gray) Torr. f. *purpureum* (Woot. & Standl.)
Lundell, comb. nov.

Rulosma purpureum Woot. & Standl., Contrib. U. S. Nat. Herb. 16:143. 1913.

TEXAS: Pecos County, off U. S. Highway 290, 9 miles west of Fort Stockton, on rocky plains, April 15, 1941, C. L. Lundell and Amelia A. Lundell 10196, perennial herb, corolla rose-red, drying reddish-purple.

The pedicels, calyx and petals are rose-red while the typical form of the species has green pedicels and calyx and bright yellow petals. No other consistent differences are evident.

Amanoa potamophila Croizat, sp. nov.

Arbor 30-pedalis, glabra, ramis more generis cicatricosis, cortice pallido. Foliis coriaceis brunneis subconcoloribus, supra quam subtus magis venosis, lanceolatis vel obovatis, 6-14 cm. longis, 2.5-6 cm. latis, nervis ca. 10-jugis, petiolo canaliculato eglanduloso ca. 1 cm. longo. Fructu tantum viso: pedicello

valido tereti ligneo recto ad 1 cm. longo, columella angulata valida semine ca. 14 mm. longo, 11 mm. lato.

A glabrous tree, the ultimate branchlets bearing large scars from the fallen leaves, bark rugulose light-brownish to grayish. Leaves coriaceous, finely veined on both faces, more so above, broadly lanceolate or obovate or elliptic, rounded at the tip, cuneate at the base, entire or subentire at the margin, 6 to 14 cm. long, 2.5 to 6 cm. broad, veins about 10 on each side, manifestly anastomosing close to the margin; petiole canaliculate glandless about 1 cm. long. Flowers not seen, only mature fruits: pedicel robust woody, stiffly erect to patent ca. 1 cm. long, columella angled, robust to 15 mm. long, valves of the endocarp woody, hard about 20 mm. long, 10 mm. broad, epicarp when dry ca. 2 mm. thick, seed brownish-marmorate smoothish impressed-retuse at the tip, about 14 mm. long, 11 mm. broad, hilum subcentral large ecarunculate.

BRITISH HONDURAS: Cattle Landing, August 27, 1933, *W. A. Schipp 1204* (type in the herbarium of the Arnold Arboretum of Harvard University).

This new species is probably conspecific with the material from British Honduras which Standley (in *Trop. Woods* 32:15, 1932) interprets as *A. grandiflora*. It amply differs from this and other species of the genus in the range and several characters, such as the length of the pedicel, the thickness of the epicarp and the size of the seed. The seed in my plant is longer than broad whereas it is about as broad as long in *A. grandiflora* Muell.-Arg. and *A. guianensis* Aublet.

Euphorbia Lundelliana Croizat, sp. nov.

Arbuscula, foliis ellipticis vel oblanceolato-ellipticis utrinque acuminatis apice aristulato-mucronatis subtus plus minusve pubescentibus supra glabris, 5-9 cm. longis, 2-3 cm. latis, petiolo ca. 1 cm. longo. Fructu tantum viso submaturo, calyculo 3-lobato, lobis acuminatis vix 2 mm. longis, gynophoro ca. 10 mm. longo, capsula glabrescenti trigono-alata ca. 27 mm. longa, 30 mm. lata.

A small tree about 4 m. tall, the innovations hispid-velutinous with a grayish pubescence. Leaves elliptic to oblanceolate-elliptic, olivaceous, chartaceous, almost evenly acuminate at both ends, aristulate-mucronate at the tip, quite entire at the margin, 5 to 9 cm. long, 2 to 3 cm. broad, puberulous to hispid below especially along the midrib, glabrate above, veins very slender patent about 10 to 20 on each side of the blade, petiole canaliculate pubescent eglandular about 1 cm. long gradually merging with the base of the blade. Inflorescences not seen, only a nearly ripe fruit: cyathium (apparently; only part of it left on the gynophore) ca. 2.5 mm. long, calyculus 3-lobed, the lobes acuminate barely 2 mm. long, gynophore robust about 10 mm. long, capsule glabrescent winged-trigonus about 27 mm. long, 30 mm. broad.

MEXICO: Chiapas, between Mazapa and Motozintla, altitude 1200 m., July 19, 1941, *Eizi Matuda 4844* (type in the herbarium of the Arnold Arboretum of Harvard University).

Manifestly allied with the "Palo Amarillo" (*Euphorbia fulva* Stapf; see Hook Ic. 34: Pl. 3324. 1936), with *E. calyculata* H.B.K., both from Mexico, and more distantly with *E. cestrifolia* H.B.K. from Peru and Colombia. *Euphorbia Lundelliana* and *E. fulva* are immediately identified by the large size of their capsule but the former is pubescent and probably more delicate in all parts than the latter.

***Sapium nitidum* (Monachino) Lundell, comb. nov.**

Sapium biglandulosum (Aubl.) Muell.-Arg. var. *nitidum* Monachino, Bull. Torrey Bot. Club 67:771. 1940.

BRITISH HONDURAS: El Cayo District, Camp 6, on hillside, May 9, 1938, Percy H. Gentle 2590, tree, 8 inches in diameter. GUATEMALA: Department of Peten, Fallabon-Yaxha road, in forest, March 22, 1933, C. L. Lundell 2192, a small tree about 8 meters high.

These, like various other collections of *Sapium* from northern Central America, have been referred to *S. jamaicense* Sw., a species not definitely known on the continent.

***Sapium Schippii* Croizat, sp. nov.**

Arbor, foliis ellipticis apice valde glandulosis, margine subintegris 6-9 cm. longis, 2-3 cm. latis, nervis patentibus ca. 15-jugis, petiolo ca. 2-3 cm. longo. Fructu tantum viso, bene pedicellato, pedicello 6-8 mm. longo, columella 7 mm. longa, epicarpio tenui, semine arillo coccineo praedito 7 mm. longo, 5 mm. lato.

A tree about 20 m. tall, about 45 cm. thick at the base of the trunk. Leaves elliptic brownish, rather broadly rounded at the apex and here bearing a manifest gland turning upwards, rotundate-cuneate at the base nearly entire to entire at the margin, 6 to 9 cm. long, 2 to 3 cm. broad, veins spreading about 15 on each side, petiole slender 2 to 3 cm. long bearing at the tip a pair of pedicelled glands. Flowers not seen: fruit a thickish rounded capsule with a pedicel in fruit 6 to 8 mm. long, epicarp thin smooth dark-olivish, cells after dehiscence about 9 mm. long, hard subwoody, seed with a reddish aril, 7 mm. long, 5 mm. broad, columella 7 mm. long.

BRITISH HONDURAS: Toledo District, Forest Home, Punta Gorda, Sept. 28, 1932, W. A. Schipp 1049 (type in the herbarium of the Arnold Arboretum of Harvard University).

Nothing in the description and the available material of *S. macrocarpum* Muell.-Arg., *S. pedicellatum* Hub., *S. Tuerckheimianum* Pax & Hoffm., *S. appendiculatum* (Muell.-Arg.) Pax & Hoffm., *S. biloculare* (Wats.) Pax, *S. lateriflorum* Hemsl. suggests this new species. It is certainly not *S. jamaicense* Jacq. for which it was distributed, as that species has very different leaves and a greenish, not reddish, aril. The rather small leaves with the reflexed tip and the long pedicels of the fruits are characteristic.

***Hypericum aphyllum* Lundell, sp. nov.**

Herba annua, erecta, glabra, caulibus gracilibus subaphyllis. Folia squami-

formia linearis-subulata, ad 2.5 mm. longa, punctata. Flores sessiles vel subsessiles. Sepala 5, linearis-subulata, ca. 2 mm. longa. Petala 5, ca. 2.5 mm. longa. Stamina 5 vel 6. Capsula 3-4.5 mm. longa. Semina parva, ca. 0.25 mm. longa.

Erect wiry annual up to 65 cm. high, glabrous throughout; branches few, slender, erect, punctate. Leaves decussately-opposite, reduced to linear-subulate appressed scales up to 2.5 mm. long, punctate. Flowers small, scattered along the erect branchlets, sessile or subsessile. Sepals 5, linear-subulate, about 2 mm. long. Petals 5, linear, about 2.5 mm. long, inflexed at apex, yellow. Stamens 5 or 6, shorter than the petals, the filaments free. Ovary with numerous ovules (up to 75); styles 3, free, about 1 mm. long, persistent. Capsule fusiform, slender, 3 to 4.5 mm. long. Seed minute, oblong, about 0.25 mm. long, almost smooth, the pits and striae obscure.

BRITISH HONDURAS: Toledo District, Monkey River, in open pine ridge near Jenkins Creek, Sept. 26, 1942, Percy H. Gentle 4175 (type in the University of Michigan Herbarium), herb, flowers yellow.

H. aphyllum, which approaches *H. gentianoides* (L.) B. S. P., differs primarily from that species in seed characteristics. The seed of the latter are 0.75 mm. long and conspicuously striate and pitted, while those of *H. aphyllum* are only 0.25 mm. long and almost smooth. The number of seed in a capsule of *H. aphyllum* often exceeds 70 or twice the maximum number in the other species.

G. V. Nash 1972 and *J. B. McFarlin* 5915 from Florida are referable here. Hence *H. aphyllum* appears to be the southern representative of the complex.

Calypttranthes cuneifolia Lundell, sp. nov.

Arbor parva, ramulis novellis sericeis. Folia petiolata, petiolo ad 5 mm. longo, lamina novella parce sericea, pallida, coriacea, elliptica, oblongo-elliptica, vel obovato-elliptica, 3.5-6.5 cm. longa, 1.5-3 cm. lata, apice obtusa vel rotundata, basi cuneata vel acuta. Inflorescentiae axillares, ad 4 cm. longae. Pedicelli fructiferi 2-6 mm. longi. Bacca sericea.

Small tree, 15 cm. in diameter; branchlets slightly compressed, brownish, sericeous at first, glabrescent early; branches stout, rigid, with short internodes. Petioles canaliculate, up to 5 mm. long, sericeous at first. Leaf blades coriaceous, pallid, elliptic, oblong-elliptic, or obovate-elliptic, 3.5 to 6.5 cm. long, 1.5 to 3 cm. wide, apex obtuse or rounded, base cuneate or acute, decurrent, somewhat sericeous at first, glabrescent early, punctate, finely reticulate veined on undersurface, the costa impressed on upper surface below the middle, prominent on undersurface, primary veins slender, 7 to 9 on each side. Inflorescence axillary, small, not over 4 cm. long in fruit, few-flowered, sericeous; peduncles solitary in the axils, subterete, up to 2.5 cm. long. Fruiting pedicels 2 to 6 mm. long. Immature fruits globose, sericeous.

BRITISH HONDURAS: Toledo District, Monkey River, in pine ridge along Jenkins Creek, August 30, 1942, Percy H. Gentle 4096 (type in the University of Michigan Herbarium), tree, 6 inches in diameter.

The British Honduran tree is allied to *C. Tonduzii* Donn. Sm. of Costa Rica. The leaves obtuse or rounded at apex and cuneate at base, the small axillary inflorescence, and the fruiting pedicels up to 6 mm. long serve to distinguish the species.

Eugenia ardisioides Lundell, sp. nov.

Arbor parva, ramulis gracilibus, minute puberulis. Folia petiolata, petiolo 3-7 mm. longo, lamina membranacea, late elliptica vel oblanceolato-elliptica, 6-13 cm. longa, 2.8-5.5 cm. lata, apice subacuminata, acumine obtuso, basi acuta, glabra. Flores breviter racemosi. Pedicelli fructiferi 2.5-5 mm. longi. Fructus globosus, ca. 6 mm. diam.

Small tree, 10 cm. in diameter; branchlets slender, subterete, slightly compressed at the nodes, minutely puberulent, drying brown. Petioles slender, subterete, 3 to 7 mm. long, minutely puberulent. Leaf blades membranaceous, elliptic or oblanceolate-elliptic, 6 to 13 cm. long, 2.8 to 5.5 cm. wide, apex obtusely subacuminate, base acute, decurrent, glabrous, costa plane or slightly impressed above, prominent beneath, primary veins 7 to 9 on each side, evident above, conspicuous beneath but not prominent. Flowers in axillary racemes; the racemes solitary or fasciculate, minutely puberulent, the rachis less than 1 cm. long. Pedicels slender, minutely puberulent, 2.5 to 5 mm. long. Fruits globose, about 6 mm. in diameter, the persistent calyx lobes 4, subequal, depressed-orbicular, up to 1.5 mm. long, ciliolate.

BRITISH HONDURAS: Toledo District, Monkey River, Jenkins Creek, in hammock in pine ridge, August 23, 1942, Percy H. Gentle 4081 (type in the University of Michigan Herbarium), tree, 4 inches in diameter, vernacular name, *broad leaf blossom berry*.

E. ardisioides and *E. oblanceifolia* Lundell are closely allied and very similar in pubescence and in size and form of the inflorescence. They differ considerably in leaf form, the former having broadly elliptic, the latter narrowly oblanceolate blades. Further, the persistent calyx lobes are depressed-orbicular in *E. ardisioides*, ovate-oblong and smaller in the other species.

Eugenia flavoviridis Lundell, sp. nov.

Arbor parva, ramulis novellis rufo-puberulis. Folia petiolata, petiolo 5-11 mm. longo, lamina chartacea vel subcoriacea, flavida, anguste oblonga, lanceolata, vel oblongo-elliptica, 4-12.5 cm. longa, 2-4 cm. lata, apice attenuata, acuminata, acumine obtuso, basi acuta. Flores breviter racemosi vel fasciculati. Pedicelli fructiferi 1.5-4 mm. longi. Fructus globosus, ca. 6 mm. diam.

Small tree, up to 7.5 cm. in diameter; branchlets slender, somewhat compressed at the nodes, puberulent with reddish hairs; older branches reddish, terete, glabrescent. Petioles canaliculate, 5 to 11 mm. long, sparsely puberulent above at first, glabrescent early. Leaf blades chartaceous or subcoriaceous, yellow-green when mature, red when young, narrowly oblong, lanceolate, or oblong-elliptic, 4 to 12.5 cm. long, 1.8 to 4.8 cm. wide, apex obtusely acumi-

nate, base acute, decurrent, the youngest leaves sparsely puberulent on upper surface along midvein, glabrous otherwise, punctate, costa impressed above, prominent beneath, the primary veins 6 to 10 on each side, slender, scarcely evident on upper surface, inconspicuous on lower surface. Inflorescence small, axillary, puberulent, the flowers in short racemes or fasciculate; calyx (in bud) glabrous, the sepals ciliolate. Fruiting pedicels 1.5 to 4 mm. long. Fruits globose, glabrous, about 6 mm. in diameter (approaching maturity).

BRITISH HONDURAS: Toledo District, Monkey River, Jenkins Creek, in hammock in pine ridge, August 25, 1942, Percy H. Gentle 4085 (type in the University of Michigan Herbarium), tree, 2 inches in diameter, berries sour; same locality and habitat, Sept. 5, 1942, Gentle 4123, tree, 3 inches in diameter, vernacular name, *pine ridge spice*; same locality and habitat, Sept. 5, 1942, Gentle 4126, tree, 3 inches in diameter, vernacular name, *pine ridge axemaster*; same locality and habitat, Sept. 27, 1942, Gentle 4178, small tree, berries sour.

From *E. flavifolia* Standl., to which it has affinity, the species differs in having thinner narrower leaves with inconspicuous venation, much smaller inflorescences, and shorter pedicels. The leaves of Gentle 4123 are a third smaller than those of the other collections.

Eugenia mouririoides Lundell, sp. nov.

Arbor parva, omnino glabra, ramulis gracilibus rigidis brunneis. Folia breviter petiolata, petiolo crasso ad 2.5 mm. longo, lamina coriacea, subtus pallidior, elliptica, oblonga, vel suborbicularia, 5-10 cm. longa, 2-5.5 cm. lata, apice abrupte acuminata, acumine obtuso, basi rotundata, subcordata, vel obtusa. Flores in axillis foliorum vel ad nodos defolios fasciculati, pedicellis 1-7 mm. longis. Sepala 3-4 mm. longa. Petala suborbicularia, ca. 6.5 mm. longa, ciliata.

Small glabrous tree 12.5 cm. in diameter, branchlets rather slender, rigid, terete, slightly compressed at the nodes, drying brown. Leaves subsessile, the petioles thick, canaliculate, up to 2.5 mm. long. Leaf blades coriaceous, olive green above, paler beneath, almost white on undersurface at first, elliptic, oblong, or suborbicular, 5 to 10 cm. long, 2 to 5.5 cm. wide, apex abruptly acuminate or apiculate, the acumen obtusish, base rounded, subcordate, or obtuse, costa impressed above, prominent beneath, primary veins inconspicuous. Flowers fasciculate, usually borne at the nodes on older wood, sometimes axillary; buds obpyriform, 4 mm. long. Pedicels 1 to 7 mm. long. Sepals ovate-oblong, 3 to 4 mm. long, apex rounded. Petals suborbicular, about 6.5 mm. long, ciliate. Stamens numerous, about 7 mm. long.

BRITISH HONDURAS: Toledo District, Monkey River, Jenkins Creek, in hammock in pine ridge, Sept. 11, 1942, Percy H. Gentle 4142 (type in the University of Michigan Herbarium), tree, 5 inches in diameter, flowers white, vernacular name, *wild guava*.

This remarkably distinct species is nearest *E. Gentlei* Lundell of the same region. From the latter it differs in having terete twigs, larger leaves, and pedicellate flowers.

Eugenia oblanceifolia Lundell, sp. nov.

Arbor parva, ramulis gracilibus rigidis, minute puberulis. Folia petiolata, petiolo 4-6 mm. longo, lamina membranacea vel subchartacea, oblanceolata vel

oblongo-oblancoolata, 4-8.5 cm. longa, 1.3-3 cm. lata, apice attenuata, obtusa, basi attenuata, acuta. Flores breviter racemosi. Pedicelli fructiferi 2.5-6 mm. longi. Fructus globosus, ca. 6 mm. diam.

Small tree, 4 cm. in diameter; branchlets slender, wiry, subterete, slightly compressed at the nodes, minutely puberulent. Petioles slender, subterete, minutely puberulent, 4 to 6 mm. long. Leaf blades membranaceous or subchartaceous, oblanceolate or oblong-oblancoolata, 4 to 8.5 cm. long, 1.3 to 3 cm. wide, apex attenuate, obtuse, base attenuate, acute, at first minutely puberulent along the midvein, entirely glabrous otherwise, costa plane or slightly impressed above, prominent beneath, primary veins slender, 9 to 12 on each side, laxly reticulate. Flowers in short axillary racemes; the racemes usually solitary, minutely puberulent, the rachis subequaling the petioles, the bracts minute, inconspicuous. Fruiting pedicels minutely puberulent, slender, 2.5 to 6 mm. long. Fruits globose, about 6 mm. in diameter, the persistent calyx lobes 4, unequal, up to 1.3 mm. long, ciliolate, apex rounded.

BRITISH HONDURAS: Toledo District, Monkey River, Jenkins Creek, in hammock in pine ridge, August 18, 1942, *Percy H. Gentle 4078* (type in the University of Michigan Herbarium). tree, 1½ inches in diameter, vernacular name, *narrow leaf blossom berry*.

The species is noteworthy for its thin narrowly oblanceolate leaves and the indument of minute hairs.

***Myrcia longicaudata* Lundell, sp. nov.**

Arbor parva, ramulis gracilibus, dense strigosis. Folia petiolata, petiolo ad 3 mm. longo, lamina membranacea, lanceolata vel oblongo-lanceolata, 6-15 cm. longa, 2.7-5 cm. lata, apice subabrupte caudato-acuminata, acumine obtuso, falcato, basi obtusa vel rotundata, supra sericea et ad costam breviter pilosa, subtus parce strigosa. Paniculae axillares, laxae multiflorae, ad 10.5 cm. longae, pedunculatae, ramulis strigillosis. Hypanthium ca. 1 mm. longum, dense strigillosum, calycis limbo patente, lobis 5, sericeis, ciliatis. Petala suborbicularia, ca. 3 mm. longa, extus parce sericea.

Small tree, branchlets slender, terete, compressed at the nodes, densely strigose with long closely appressed hairs, drying brown. Petioles short, up to 3 mm. long, shallowly canaliculate, brown pilose above, coarsely subappressed strigose beneath. Leaf blades membranaceous, concolorous, lanceolate or oblong-lanceolate, 6 to 15 cm. long, 2.7 to 5 cm. wide, apex subabruptly caudate-acuminate, the acumine obtuse or rounded, sericeous above at first, the hairs along the midvein finer and persistent, sparsely strigose on undersurface, the hairs coarser and denser along the midvein, finely reticulate veined, the costa slightly impressed above, prominent beneath, primary veins 14 to 16 on each side, slender, conspicuous. Panicles axillary, solitary or fasciculate, lax, many-flowered, up to 10.5 cm. long, pedunculate, the branches strigillose, the terminal cymules open; flowers subsessile. Hypanthium about 1 mm. long, densely strigillose; calyx limb reflexed in flower, sericeous, 5-lobed, the lobes triangular or broadly ovate, less than 1 mm. long, ciliate. Petals sparsely sericeous outside, suborbicular, about 3 mm. long. Receptacle and base of style pubescent.

HONDURAS: Lancetilla Valley, Lancetilla, June 22 to July 27, 1929, *A. M. Chickering 153* (type in the University of Michigan Herbarium), low spreading tree.

The species is noteworthy for the strigose indument, large membranaceous caudate-acuminate leaves, and the lax ample inflorescences borne in the leaf axils of at least six of the terminal nodes.

Myrcia Schippii Lundell, sp. nov.

Arbor parva, ramulis gracilibus, subteretibus, sericeis. Folia petiolata, petiolo 2.5-5 mm. longo, lamina subcoriacea vel coriacea, supra ad costam breviter pilosa, subtus sericea, elliptica, oblongo-elliptica, vel lanceolata, 4-11.5 cm. longa, 1.5-4 cm. lata, apice obtuse apiculata, subacuminata, vel attenuata, basi rotundata, obtusa, vel acuta. Paniculae axillares et terminales, ad 5.5 cm. longae, pedunculatae, ramulis parce sericeis. Pedicelli fructiferi ad 1.5 mm. longi. Hypanthium dense sericeum, calycis limbo patente sericeis, lobis 5, ciliolatis. Petala alba, suborbicularia, 3 mm. longa, extus parce sericea. Bacca ellipsoidea, ca. 8.5 mm. longa, parce sericea.

Small tree, up to 15 cm. in diameter; branchlets slender, sericeous, subterete, somewhat flattened, drying reddish-brown. Petioles short, 2.5 to 5 mm. long, sericeous. Leaf blades subcoriaceous to coriaceous, short pilose along the midvein above, the upper surface otherwise glabrous, the lower surface thinly sericeous, the hairs denser along the costa, elliptic, oblong-elliptic, or lanceolate, 4 to 11.5 cm. long, 1.5 to 4 cm. wide, apex abruptly apiculate, subacuminate, or attenuate, the tip obtuse or obtusish, base rounded, obtuse, or acute, finely reticulate veined on both surfaces, costa impressed above, prominent beneath, primary veins slender, 10 to 19 on each side. Panicles axillary and terminal, small, up to 5.5 cm. long, reddish, thinly sericeous; peduncles up to 2.5 cm. long. Flowers white, subsessile, the pedicel in fruit up to 1.5 mm. long. Hypanthium about 1 mm. long, densely sericeous; calyx limb spreading, 5-lobed, the lobes thinly sericeous, ciliolate, depressed-ovate, scarcely 1 mm. long, rounded or subtruncate. Petals thinly sericeous outside, suborbicular, 3 mm. long. Stamens glabrous, up to 5 mm. long. Receptacle and base of style pubescent. Fruits broadly ellipsoid, about 8.5 mm. long, sparsely sericeous.

BRITISH HONDURAS: Stann Creek District, All Pines, in open pine ridge, June 2, 1931, *W. A. Schipp 797* (type in the University of Michigan Herbarium), small tree, 25 feet high, 3 inches in diameter, flowers white, sweetly perfumed; near Mangrove Creek, in broken ridge, Sept. 4, 1940, *Percy H. Gentle 3397*, tree, 2 inches in diameter, vernacular name, *pigeon plum*. Toledo District, Monkey River, in hammock in pine ridge near Jenkins Creek, Sept. 20, 1942, *Percy H. Gentle 4159*, tree, 6 inches in diameter, vernacular name, *pine ridge cinnamon*.

The coriaceous leaves glabrous above except along the midvein, the fine appressed silky indument, and the small inflorescence well mark the species. The leaf blades vary considerably in shape; in the type they are predominantly elliptic, up to 7.5 cm. long, 4 cm. wide, with the apex abruptly apiculate or obtusely subacuminate. In *Gentle 3397* and *4159*, the blades are oblong-elliptic or lanceolate, somewhat longer, and attenuate at the apex. *Schipp 797* was distributed as *M. Oerstediana* Berg., a closely allied species of Costa Rica.

Psidium Gentlei Lundell, sp. nov.

Frutex parva, ramulis puberulis. Folia breviter petiolata, petiolo raro ad 1.5 mm. longo, lamina subcoriacea, lanceolata vel oblongo-lanceolata, 1.5-5.5 cm. longa, 1-2.4 cm. lata, apice acuta, basi rotundata, ciliata. Pedunculi ad 1.8 cm. longi. Bacca glabra, globosa.

Low shrub with thick underground stem; branches erect, slender, puberulent, drying reddish-brown. Leaves subsessile, the petioles rarely up to 1.5 mm. long. Leaf blades subcoriaceous, lanceolate or oblong-lanceolate, 1.5 to 5.5 cm. long, 1 to 2.4 cm. wide, apex usually attenuate, acute or subacuminate, base usually rounded, sometimes acutish, appressed ciliate at first, entirely glabrous otherwise, costa plane above, prominent beneath, primary veins 5 or 6 on each side, evident but inconspicuous. Peduncles axillary, solitary, slender, up to 1.8 cm. long, puberulent, 1- or rarely 2-flowered, bearing 2 bractlets at apex; bractlets linear-lanceolate, about 5 mm. long, ciliate. Fruits globose, 1.2 cm. in diameter (immature); persistent calyx limb 4- or 5-lobed, the lobes depressed-ovate, about 3 mm. long, glabrous outside, ciliate, sericeous inside.

BRITISH HONDURAS: Toledo District, Monkey River, Jenkins Creek, in open pine ridge, August 1, 1942, Percy H. Gentle 4062 (type in the University of Michigan Herbarium), perennial, flowers white, vernacular name, wild guava.

The short peduncles, the ciliate but otherwise glabrous leaves, the glabrous fruits, and the lanceolate leaf blades serve to distinguish *P. Gentlei* from *P. Oerstedianum* Berg., the species to which it has close affinity. *P. Oerstedianum*, as revealed by the type photograph and specimens available from British Honduras, has obovate or broadly elliptic pubescent leaves, peduncles twice as long, pubescent fruits, and calyx lobes pubescent outside.

Tibouchina belizensis Lundell, sp. nov.

Frutex, ramis denseque squamosis. Folia petiolata, petiolo 2-4 mm. longo, lamina coriacea, rigida, ovata vel ovato-oblonga, 2-4.5 cm. longa, 1-2.8 cm. lata, apice acuta, basi rotundata vel subcordata, integra, 3-nervia, raro 5-nervia, utrinque setulosa. Bracteae exteriores ca. 3 mm. longae, interiores ca. 5.5 mm. longae. Calycis tubus ca. 7 mm. longus; lobi ad 7 mm. longi. Petala obovata, 1.5 cm. longa, apice ciliata, apiculata. Stylus 1.5 cm. longus.

Low shrub with erect branches; branchlets white at first, becoming brown, covered with small appressed lacerate-lanceolate scales. Petioles short, scaly, 2 to 4 mm. long. Leaf blades coriaceous, yellowish, slightly paler beneath, ovate or ovate-oblong, 2 to 4.5 cm. long, 1 to 2.8 cm. wide, apex acute, base rounded or subcordate, margin entire, usually 3-nerved, sometimes 5-nerved, the veins impressed above, prominent beneath, setulose on both surfaces, the veins and margin scaly on undersurface. Flowers 5-merous, solitary or glomerate, usually borne in open terminal leafy panicles. Calyx subtended by an involucre of two pairs of fused bracts, the bracts obovate, fused to above the middle, the lower outer pair about 3 mm. long, the inner upper pair about 5.5 mm. long, apiculate, covered outside with small lacerate-lanceolate appressed scales; calyx tube

about 7 mm. long, glabrous inside, covered outside with white imbricate narrowly lanceolate scales up to 4 mm. long, the scales lacerate and cuspidate; calyx lobes 5, ovate, attenuate to the apex, 7 mm. long including the filiform apical cusp, minutely scaly. Petals pink, obovate, 1.5 cm. long, apex ciliate and apiculate. Stamens 10, subequal, glabrous, the filaments 1 cm. long, the anthers arcuate, attenuate, the connective conspicuously prolonged at base and bilobed. Ovary 5 mm. long, appressed scaly at apex, glabrous below, 5-sulcate; style glabrous, 1.5 cm. long.

BRITISH HONDURAS: Toledo District, Cow Pen, under oak trees in pine ridge, Sept. 17, 1942, Percy H. Gentle 4155 (type in the University of Michigan Herbarium), flowers pink, scented and showy, vernacular name, *small leaf sirin*; same locality and habitat, August 15, 1942, Gentle 4074, vernacular name, *small leaf sirin*.

This remarkable addition to the flora of British Honduras belongs to the section Eutibouchina with affinity to *T. aspera* Aubl. of northern South America. The small involucre bracts of the calyx, and leaves usually 3-nerved serve to distinguish the species.

Malea Lundell, gen. nov. *Ericacearum*

Frutex epiphyticus, laminis coriaceis alternis breviter petiolatis pinnatinerviis. Inflorescentiae axillares, solitariae, racemosae, sessiles vel subsessiles. Calyx cum pedicello articulatus, tubo subcampanulato, limbo 5-lobato. Corolla subcylindrica, parva, 5-lobata. Stamina 10 quam corolla leviter breviora, filamentis distinctis, antheris ca. 4 mm. longis, tubulis loculos subaequantibus. Ovarium 10-loculare.

Type species, *Malea pilosa* Lundell.

Upon the basis of the peculiarity of its ovary, Dr. A. C. Smith, who has examined our material, excludes the plant from the Thibaudieae. Under the Thibaudieae, *Malea* would key out to either *Gonocalyx* or *Thibaudia*; aside from the characteristics of the ovary, the elongate anther pores would exclude it from the former, while the slender tubules would exclude it from the latter. The affinity of the genus to *Gaylussacia* seems probable. Its distinctive characteristics are the incompletely 10-celled ovary usually with 2 ovules in each cell, the calyx articulate with the pedicel, the small imbricated bractlets at the base of the inflorescence, the small subcylindric corolla with short erect oblongish lobes, the free filaments, and the free thin slender tubules subequaling the scabridulous anther sacs.

The genus is named for Mt. Malé, the type locality.

Malea pilosa Lundell, sp. nov.

Frutex epiphyticus, pubescentibus. Folia petiolata, 2.5-6 mm. longo, lamina coriacea, lanceolata, 3-7.5 cm. longa, 0.8-3 cm. lata, apice obtusa, basi rotundata vel obtusa, subintegra, pilosa. Inflorescentia multiflora, breviter racemosa, pilosa, pedicellis ad 7 mm. longis. Calyx subcampanulatus, lobis ca. 1.3 mm. longis, acutis. Corolla 8-10 mm. longa, extus pilosa, lobis ad 3 mm. longis, obtusis. Filamenta pilosa. Antheris parvis, basi attenuatis. Ovarium 10-loculare.

An epiphytic shrub, pubescent throughout; branches rather stout, crowded, subterete, elongate with short internodes, drying blackish, persistently hairy. Petioles stout, 2.5 to 6 mm. long. Leaf blades coriaceous, slightly shiny above, dull on undersurface, lanceolate, usually 3 to 5 cm. long, sometimes up to 7.5 cm. long, usually 0.8 to 1.8 cm. wide, sometimes up to 3 cm. wide, apex obtuse, base usually rounded, sometimes obtuse, margin thickened, subentire, bearing few minute remote glandular teeth, persistently pilose on undersurface, puberulent or short pilose on upper surface at first with incurved hairs, glabrescent with age, reticulate veined on both surfaces, costa and primary veins elevated, conspicuous but not prominent, the primary veins 4 to 6, anastomosing near the margin. Inflorescence axillary, solitary, short racemose, sessile or subsessile, with small imbricate bractlets at base, the rachis up to 7.5 mm. long, usually less than 5 mm. long, pilose. Pedicels slender, crowded, pilose, up to 7 mm. long, subtended by a lanceolate-triangular persistent bractlet about 1.2 mm. long, bearing a pair of persistent lanceolate opposite or subopposite bractlets at or below the middle. Calyx pilose, the tube subcampanulate, abruptly articulate with the pedicel, the limb 5-lobed, the lobes narrowly triangular, about 1.3 mm. long, acute. Corolla subcylindric, only slightly ampliate above, 8 to 10 mm. long, pilose outside, 5-lobed, the lobes erect or suberect, up to 3 mm. long, obtuse. Stamens 10, equal, slightly shorter than the corolla; filaments pilose, coherent at base only, attached at base of corolla; anthers attached dorsally at middle, about 4 mm. long, attenuate at base, the apex with two free slender tubules slightly shorter than the sacs or equaling them, opening by elongate introrse clefts, the sacs scabridulous. Ovary inferior, incompletely 10-celled, usually with 2 ovules in each cell; disk annular; style slender, equaling the corolla. Fruits unknown.

MEXICO: Chiapas, Mt. Malé, near Porvenir, altitude 3200 m., July 6 to 12, 1941, *Eizi Matuda 4614* (type in the University of Michigan Herbarium), on tree, flowers white; Rodeo, near Siltepec, altitude 2800 m., August 1 to 5, 1941, *Matuda 4580*, flowers white.

Although the collector describes the flowers as white, the corollas are salmon-pink when dry.

Ardisia amanuensis Lundell, sp. nov.

Frutex, ramulis furfuraceo-lepidotis. Folia petiolata, petiolo marginato, ad 5 mm. longo, lamina chartacea, obscure crenulata, oblanceolato-elliptica vel elliptica, 6-11.5 cm. longa, 2.5-5 cm. lata, apice abrupte breviter acuminata, basi subcuneata, supra glabra, subtus lepidota. Inflorescentia late paniculata, furfuraceo-lepidota, ca. 7 cm. longa. Pedicelli 3-4 mm. longi. Flores umbellati, 4-meri. Calyx 1.8 mm. longus, lobis ovatis. Corolla 5 mm. longa, lobis oblongo-ellipticis. Antherae 3 mm. longae. Fructus globosus, 5-6 mm. diam.

Shrub, about 5 m. high; branchlets rather slender, subterete, at first furfuraceous-lepidote. Petioles short, marginate, up to 5 mm. long. Leaf blades chartaceous, obscurely crenulate, oblanceolate-elliptic or elliptic, 6 to 11.5 cm. long, 2.5 to 5 cm. wide, apex abruptly short acuminate, base subcuneate, decur-

rent, lepidote on undersurface, costa plane above, prominent beneath, primary veins conspicuous, 8 to 11 on each side, reticulate veined. Inflorescence terminal, paniculate, pyramidal, furfuraceous-lepidote, about 7 cm. long. Pedicels 3 to 4 mm. long. Flowers umbellate, numerous, crowded, 4-parted; buds slender, fusiform. Calyx lepidote, punctate, about 1.8 mm. long, the 4 lobes ovate, rounded at apex, minutely ciliolate. Corolla 5 mm. long, few punctate, deeply 4-lobed, the lobes oblong-elliptic. Anthers 3 mm. long, concolorous, apically dehiscent; filaments 1.2 mm. long. Ovary glabrous; style 4.5 mm. long. Fruits globose, 5 to 6 mm. in diameter.

PANAMA: Bocas del Toro Province, vicinity of Chiriqui Lagoon, Old Bank Island, Feb. 14, 1941, *H. von Wedel 2088* (type in the University of Michigan Herbarium), shrub, 15 ft. high, flowers white; Isla Colon, Old Bank Island, Feb. 21, 1941, *Wedel 2135*, shrub, 18 ft. high, fruit red.

The species most closely resembles *A. Maxonii* Standl. of the subgenus *Icacorea*, but differs in its abruptly acuminate larger leaves, furfuraceous-lepidote indument, and shorter pedicels. The flowers are 4-parted.

Ardisia glomerata Lundell, sp. nov.

Arbor parva (?); ramulis crassis, ca. 1 cm. diam., ferrugineo-tomentosis. Folia magna, petiolata, petiolo marginato, 2-3 cm. longo, lamina chartacea, oblanceolato-elliptica, 36.5 cm. longa, 14 cm. lata, apice acuminata, margine integra, supra glabra, subtus dense furfuraceo-lepidota. Inflorescentia paniculata, ca. 25 cm. longa, furfuracea. Flores glomerati. Pedicelli crassi, 1-5 mm. longi. Calyx ca. 4 mm. longus. Corolla 9 mm. longa, lobis oblongis. Antherae 4 mm. longae. Ovarium glabrum.

Probably a small tree; branchlets thick, almost 1 cm. in diameter, ferruginous-tomentose. Petioles broadly marginate to base, stout, 2 to 3 cm. long, essentially glabrous above. Leaf blades large, chartaceous, drying brown, paler beneath, oblanceolate-elliptic, 36.5 cm. long, 14 cm. wide, apex acuminate, base subabruptly narrowed and broadly decurrent, entire, glabrous above, furfuraceous-lepidote beneath, the costa stout, bearing stalked stellate hairs, primary veins slender, about 40 on each side. Inflorescence terminal, large, pyramidal, paniculate, about 25 cm. long; rachis and branches stout, densely furfuraceous, ferruginous; bracts conspicuous, persistent; flowers glomerate, numerous. Pedicels stout, 1 to 5 mm. long, furfuraceous. Calyx coriaceous, furfuraceous, about 4 mm. long, the lobes depressed orbicular, about 3 mm. long, 4 to 5 mm. wide, the margin hyaline. Corolla 9 mm. long; tube about 3 mm. long; lobes punctate, oblong, about 3.5 mm. wide, margin hyaline. Anthers 4 mm. long, with subapical pores. Filaments wide, about 2 mm. long. Ovary glabrous. Style about 7.5 mm. long, punctate.

PANAMA: Coclé Province, probably in vicinity of El Valle, *P. H. Allen 2741* (type in the personal herbarium of P. H. Allen).

Ardisia Wedelii Lundell, sp. nov.

Arbor parva, ramulis crassis, ferrugineo-furfuraceo-lepidotis. Folia sessilia,

subchartacea, oblanceolata, 25-40 cm. longa, 9-12 cm. lata, apice attenuata, acuminata, basi attenuata, rotundata, supra parce et minute lepidota, subtus dense furfuraceo-lepidota. Inflorescentia anguste paniculata, longe pedunculata, ad 20 cm. longa, furfuraceo-lepidota. Flores umbellati. Pedicelli ad 4.5 mm. longi. Calyx punctatus, 2.5 mm. longus, lobis 5, acutis, ciliatis. Corolla parce lepidota, ca. 4 mm. longa, lobis ovato-lanceolata, punctata. Antherae ca. 1.7 mm. longae. Ovarium glabrum.

Small tree, about 3 m. high; branchlets thick, almost 1 cm. in diameter at apex, densely furfuraceous-lepidote, ferruginous. Leaves sessile, subchartaceous, drying brown, paler beneath, oblanceolate, 25 to 40 cm. long, 9 to 12 cm. wide, apex attenuate, acuminate, base attenuate, rounded, sparsely and minutely lepidote above, densely furfuraceous-lepidote beneath with larger scales, costa impressed above, prominent beneath, primary veins 30 to 40 on each side, conspicuous on undersurface. Inflorescence apparently terminal, long pedunculate, up to 20 cm. long including peduncle 13 cm. long, less than 2 cm. wide, densely furfuraceous-lepidote, the peduncle bearing 1 or 2 bracts below the middle. Flowers umbellate, the umbels subsessile. Pedicels furfuraceous, up to 4.5 mm. long. Calyx punctate, furfuraceous, 2.5 mm. long, deeply 5-lobed, the lobes ovate-triangular, acute, ciliate. Corolla sparsely lepidote, about 4 mm. long, lobed to below the middle, the lobes ovate-lanceolate, punctate. Anthers about 1.7 mm. long, acute, longitudinally dehiscent. Filaments subequaling anthers, filiform, expanded at base. Ovary glabrous; style about 4 mm. long.

PANAMA: Bocas del Toro Province, August 1, 1940, *H. von Wedel* 299 (type in the herbarium of the Missouri Botanical Garden), tree, about 10 ft. high, flowers purple; vicinity of Chiriqui Lagoon, Fish Creek lowlands, May 7, 1941, *Wedel* 2393, shrub, 12 ft. high, flowers maroon.

This remarkable species, noteworthy for its large sessile leaves, furfuraceous-lepidote indument, and narrow inflorescences with elongate peduncles, probably is allied to *A. palmana* Donn. Sm. of Costa Rica.

***Forestiera Wrightiana* Lundell, sp. nov.**

Frutex, ramulis novellis pubescentibus. Folia petiolata, subcoriacea, elliptica vel ovato-elliptica, 1.3-5 cm. longa, 0.7-2.4 cm. lata, apice obtusa, rotundata, vel acutiuscula, basi acuta, margine serrulata, subtus molliter pilosa. Flores laterales, dioecii. Pedicelli fructiferi 1-2 mm. longi. Bacca glauca, subglobosa, 6-10 mm. longa.

A shrub, 2 m. high, with short lateral branches; branchlets usually reduced, pubescent with short incurved hairs. Leaves opposite, crowded at the tips of the spur-like branchlets; petioles pubescent, slender, canaliculate. Leaf blades firm, subcoriaceous, elliptic or ovate-elliptic, 1.3 to 5 cm. long, 0.7 to 2.4 cm. wide, apex obtuse, rounded, or acutish, base acute, slightly decurrent, margin serrulate, densely pilose beneath over the entire surface, pubescent above along the midvein, the midvein, primary veins, and veinlets slightly impressed above, the primary veins inconspicuous beneath. Staminate flowers unknown. Pistillate flowers lateral, fasciculate or borne in reduced racemes, usually glabrous, some-

times sparsely hirtellous or densely hirtellous; pedicels 1 to 2 mm. long. Bracts elliptic, ciliate, up to 2.2 mm. long. Calyx small, usually 2- or 4-lobed, the lobes unequal. Petals not evident. Staminodia usually 4, reduced. Ovary 2-celled, with 2 ovules in each cell. Style slender. Fruits blue-black, glaucous, subglobose, 6 to 10 mm. long, depressed apically.

TEXAS: Newton County, off U. S. highway 190, in woods above Cow Creek, September 10, 1942, C. L. Lundell and S. W. Geiser 11878 (type in the University of Michigan Herbarium, duplicate in the herbarium of Southern Methodist University); same locality and date. Lundell and Geiser 11879. Harris County, Houston, in low woods, Sept. 18, 1915, E. J. Palmer 8582.

F. Wrightiana, a species closely allied to *F. ligustrina* (Michx.) Poir., commemorates the name of Charles Wright, the indefatigable botanical explorer of Texas. The shrub grows in the southeastern region where Wright as a young man made his first collections in the state.

Palmer 8582 was distributed as *Ilex verticillata* (L.) Gray.

Cordia belizensis Lundell, sp. nov.

Arbor parva; ramulis hirtellis. Folia petiolata, petiolo 3-6 mm. longo, lamina chartacea, lanceolato-oblonga, oblonga, vel obovato-oblonga, 9-18 cm. longa, 3.3-7.5 cm. lata, apice acuminata, basi rotundata, supra scabrida, subtus hirtella, margine integra vel dentata. Inflorescentia parva, laxe dichotome ramosa; calyce ad anthesin ca. 4 mm. longo, extus dense strigoso, lobis 5 triangularibus ca. 1 mm. longis. Corolla alba, ca. 6.5 mm. longa. Filamenta barbata. Ovarium puberulum. Drupa minute strigosa.

Small tree up to 10 cm. in diameter, branching dichotomous; branchlets hirtellous, terete. Leaves homomorphic; petioles densely hirtellous, 3 to 6 mm. long. Leaf blades chartaceous, lanceolate-oblong, oblong, or obovate-oblong, 9 to 18 cm. long, 3.3 to 7.5 cm. wide, apex subabruptly acuminate, base rounded, upper surface scabrid with short erect or subappressed hairs, undersurface green, hirtellous and conspicuously reticulate veined, costa and primary veins slender, conspicuous on both surfaces, coarser on undersurface, the primary veins 7 or 8 on each side, margin entire or dentate above the middle of blade. Inflorescence densely strigillose, borne usually at the forks of the stem, small, few-flowered, loosely branched, 4 to 12 cm. wide, up to 8 cm. long, the peduncles up to 2.5 cm. long. Flowers sessile, apparently perfect. Calyx in bud obovoid, about 3.5 mm. long, not ribbed, densely covered with short appressed tawny hairs, inner surface sericeous, opening by 5 triangular lobes scarcely 1 mm. long. Corolla white, the tube about 3.5 mm. long, the lobes oblong, about 3 mm. long. Filaments barbate at base; anthers oblong, about 1.7 mm. long, base lobed to the middle. Ovary puberulent above. Style included, sparsely appressed hairy, scarcely 3 mm. long, lobed above the middle. Fruiting calyx shallowly toothed, about 8 mm. in diameter, 5 mm. long, strigillose. Drupe persistently and minutely strigillose, ovoid, about 1 cm. long.

BRITISH HONDURAS: Toledo District, Monkey River, in high ridge between Swasey Branch and Waha-leaf Creek, July 5, 1942, Percy H. Gentle 4045 (type in the

University of Michigan Herbarium), tree, 4 inches in diameter, flowers white. Stann Creek District, Carib Reserve, in broken ridge, Nov. 22, 1939, Percy H. Gentle 3099, tree, 2 inches in diameter.

Although closely allied to *C. scabrifolia* A. DC. and *C. bicolor* A. DC., *C. belizensis* differs from both in the character of the indument on the under-surface of the leaf; the blade is green below and hirtellous with erect or sub-erect hairs. In Gentle 3099 the leaves are conspicuously dentate, and some leaves of the type collection also bear small teeth; both *C. scabrifolia* and *C. bicolor* have entire blades. The small inflorescence, densely strigose smooth calyx, puberulent ovary, included hairy style, and the densely and minutely strigose fruits serve to distinguish the species from other members of the section Pilicordia.

TETRACTOLEA COULTERI A. Gray, Amer. Journ. Sci., ser. 2, 16:98. 1853.

TEXAS: Hidalgo County, 12 miles northwest of Mission, on sand in scrub, April 4, 1941, C. L. Lundell and Amelia A. Lundell 9966, perennial herb, corolla pinkish.

Although the calyx lobes are filiform at apex rather than subulate, additional collections are needed to determine if the difference is of varietal importance. This is the first record for the species in the lower Rio Grande Valley.

Tetraclea viscida Lundell, sp. nov.

Annua, ca. 45 cm. alta, erecta, viscida. Folia decussata, sessilia vel subsessilia, anguste elliptica, 5-18 mm. longa, ad 9 mm. lata, apice acuta, basi 3-nervia. Cymae axillares, pedunculatae, 1- vel 2-florae. Corolla parva. Calyx fructiferus usque ad 8 mm. longus.

Erect viscid annual, about 45 cm. tall, densely puberulent with gland tipped hairs; stem and main branches drying reddish-purple; branchlets green, subterete. Leaves decussately opposite, sessile or subsessile, the petioles not over 3 mm. long, margined. Leaf blades entire, thick chartaceous, probably fleshy, narrowly elliptic, 5 to 18 mm. long, up to 9 mm. wide, broadest at the middle, apex and base acute, glandular-puberulent on both surfaces, some coarser eglandular incurved hairs intermixed, 3-nerved from the base. Cymes axillary, pedunculate, 1- or 2-flowered; peduncles up to 1 cm. long in fruit; pedicels not over 1 mm. long; the peduncles, pedicels, bracts, and calyx glandular-puberulent and sparsely hirsute with incurved hairs. Calyx campanulate, 4- or 5-lobed, 8- or 10-nerved, accrescent, up to 8 mm. long in fruit, lobed to below the middle, the lobes lanceolate, attenuate to the acute apex. Corolla apparently less than 5 mm. long (buds only available), the 4 outer lobes pubescent above the middle on the outer surface, the other lobe with a line of hairs along the midvein. Stamens 4, exserted. Ovary shallowly 4-lobed at apex. Style bifid at apex, the branches subulate, equal, reflexed. Pyrenes small, hard, obovoid, reticulate-rugose, attached at base only, minutely puberulent at apex.

TEXAS: Uvalde County, 19 miles northwest of Uvalde, altitude 1200 feet, Sept. 11, 1940, Forrest Shreve 9917 (type in the University of Michigan Herbarium).

T. Coulteri A. Gray, the only other species in the genus, is a perennial herb with eglandular pubescence, ovate petiolate leaves up to 4 cm. long, and corollas up to 1.5 cm. long. *T. viscida* differs notably in being an annual densely puberulent throughout with gland tipped hairs. It is distinguished further by thick elliptic sessile or subsessile leaves less than 2 cm. long, and small corollas and pyrenes.

Solanum ovandense Lundell, sp. nov.

Herba, ramulis glabris. Folia pinnata, longe petiolata; foliola 5, raro 3, membranacea vel subchartacea, lanceolata, ad 5.5 cm. longa, 1.5 cm. lata, apice acuminata, petiolulis lateralibus 1-3 mm. longis. Inflorescentiae extra-axillares, cymoso-paniculatae, ad 4 cm. longae. Pedicelli ca. 7 mm. longi. Calyx ca. 2 mm. longus, lobis late ovatis, apiculatis, ca. 0.5 mm. longis. Corolla 7 mm. longa. Antherae 3 mm. longae. Stylus elongatus, 7 mm. longus.

Herbaceous vine; stems rooting at the nodes; branches essentially glabrous, bearing only a few hairs at the nodes. Leaves imparipinnate, with small pseudostipules at the base of the petiole; petioles very slender, 1 to 4 cm. long, canaliculate, pubescent on upper side. Leaflets usually 5, sometimes 3, membranaceous or subchartaceous, lanceolate, up to 5.5 cm. long, 1.5 cm. wide, the terminal largest, the lower sometimes greatly reduced, apex acuminate, base acute to rounded, often unequal sided, glabrous except for a few scattered hairs chiefly along the veins; petiolule of terminal leaflet up to 5 mm. long, of lateral leaflets 1 to 3 mm. long, canaliculate and hairy on upper side. Inflorescence cymose-paniculate, extra-axillary, up to 4 cm. long, with elongate very slender peduncle, essentially glabrous. Pedicels articulate at the base, about 7 mm. long at anthesis, slender, thickened upwards. Calyx with a few appressed hairs, essentially glabrous, 2 mm. long; the lobes broadly ovate, apiculate, scarcely 0.5 mm. long, puberulent at apex. Corolla 7 mm. long, the lobes lanceolate-oblong, puberulent at apex. Anthers oblong, 3 mm. long. Ovary glabrous; style 7 mm. long.

MEXICO: Chiapas, Mt. Ovando, near Escuintla, altitude 1500 m., July 16, 1940, *Eizi Matuda* 4182 (type in the University of Michigan Herbarium).

The affinity of the species is clearly with *S. inscendens* Rydb. of the subsection *Basarthrum*. From that species *S. ovandense* differs in its essentially glabrous branches, fewer leaflets, minute apiculate calyx lobes, and larger corolla and anthers.

C. L. Lundell and Amelia A. Lundell 7185 from Chapulhuacan, Hidalgo, is interpreted as *S. inscendens* Rydb.

Solanum tacanense Lundell, sp. nov.

Herba, ramulis dense pubescentibus. Folia pinnata, petiolata; foliola 5, membranacea, lanceolata vel oblongo-lanceolata, 1-6.5 cm. longa, 0.5-2.5 cm. lata, apice attenuata, obtusa, parce hirsuta, petiolulis lateralibus 0.8-2.5 mm. longis. Inflorescentiae extra-axillares, paniculatae, ca. 3.5 cm. longae. Pedicelli

ad 7 mm. longi. Calyx ca. 2 mm. longus. Corolla 5.5 mm. longa, lobis oblongo-lanceolatis. Antherae 2.5 mm. longae. Stylus ca. 2 mm. longus.

Herbaceous vine; stems rooting at the nodes; branches densely pubescent with simple tawny hairs. Leaves imparipinnate, with pseudostipules at the base of the petiole; petioles 1.3 to 4.5 cm. long, pubescent. Leaflets 5, membranaceous, lanceolate or oblong-lanceolate, 1 to 6.5 cm. long, 0.5 to 2.5 cm. wide, the terminal largest, apex attenuate, obtuse, base acute to rounded, sparsely pubescent on both surfaces, the hairs densest along the veins; petiolule of terminal leaflet up to 8 mm. long, of lateral leaflets 0.8 to 2.5 mm. long. Inflorescence paniculate, extra-axillary, about 3.5 cm. long, pedunculate, densely tawny pubescent. Pedicels articulate at the base, up to 7 mm. long, thickened upwards, sparsely pubescent. Calyx sparsely hairy, scarcely 2 mm. long; the lobes triangular, obtuse, about 0.6 mm. long. Corolla 5.5 mm. long, the lobes oblong-lanceolate, puberulent at apex. Anthers oblong, 2.5 mm. long; filaments very short, pilose. Ovary glabrous; style about 2 mm. long, shorter than stamens.

MEXICO: Chiapas, Volcán de Tacaná, altitude 2100 m., April 2, 1939, *Eizi Matuda* 2958 (type in the University of Michigan Herbarium).

S. tacanense, referable to the subsection *Basarthrum*, is nearest *S. subvelutium* Rydb. The latter has 7- rarely 5-leaflets, longer glabrous pedicels, and corolla only 4 mm. long.

Russelia pubescens Lundell, sp. nov.

Suffruticosa, ramis ramulisque striato-angulatis, pubescentibus. Folia opposita vel ternata, breviter petiolata, membranacea vel chartacea, ovata, 2.5-10.5 cm. longa, 1.7-6.5 cm. lata, apice acutiuscula vel obtusa, basi rotundata vel subcordata, crenato-dentata, supra parce hirsuta, subtus breviter pilosa. Calyx parce pubescentibus, lobis ovatis, 3-4 mm. longis, dentatis et abrupte cuspidato-subulatis. Corolla 10-12 mm. longa. Capsula glabra.

Suffrutescent, erect, up to 1.5 m. tall; stems subterete, striate-angulate, pubescent with straight hairs of irregular length. Leaves opposite or ternate, subsessile, the petioles less than 2 mm. long. Leaf blades membranaceous or thin chartaceous, ovate, usually 2.5 to 5.5 cm. long, sometimes up to 10.5 cm. long, usually 1.7 to 4 cm. wide, sometimes up to 6.5 cm. wide, apex acutish or obtuse, base rounded or subcordate, coarsely crenate-dentate, pubescent, the hairs straight and unequal, coarser and longer on the upper surface, not resinous-punctate, conspicuously reticulate veined, costa and primary veins subimpressed above, prominent on undersurface, the primary veins 5 to 7 on each side. Peduncles axillary, up to 5 mm. long, pubescent. Bractlets subulate, up to 5.5 mm. long, pubescent. Pedicels up to 3.5 mm. long, sparsely hairy. Calyx lobes 3 to 4 mm. long, ovate, dentate and abruptly long cuspidate at the middle, sparsely hairy. Corolla crimson, tubular, constricted slightly a third above base, 10 to 12 mm. long, glabrous outside, short barbate within at base and above middle on lower side of tube, the upper lobe shallowly emarginate,

2.5 mm. long, the 3 lower lobes about 3 mm. long, rounded at apex. Stamens didymous, filaments barbate at base, the shorter 3 mm. long, the longer 3.5 mm. long, staminode about 0.7 mm. long. Capsule ovoid, glabrous.

MEXICO: Jalisco, east of San Sebastian, Hacienda del Ototal, arroyo de los Hornos, altitude 1500 m., growing in woods, March 5, 1927, *Ynes Mexia 1815* (type in the University of Michigan Herbarium).

The collection was distributed as *R. tepicensis* Robinson, a species with subappressed sparser pubescence, resinous-punctate leaf blades, calyx lobes scarcely half as long, and corolla only 6 to 7 mm. long. *R. pubescens* is allied also to *R. rotundifolia* Cav., but the small crowded cymes immediately distinguish it from that species.

Chiococca belizensis Lundell, sp. nov.

Frutex scandens, ramulis minute puberulis. Folia petiolata, petiolo ad 11 mm. longo, lamina subcoriacea vel coriacea, ovato-elliptica, ovato-oblonga, vel lanceolata, 6-12 cm. longa, 3-5.5 cm. lata, apice subabrupte acuminata, basi rotundata et abrupte acuta. Inflorescentiae axillares, paniculatae, ad 10 cm. longae, minute puberulae. Pedicelli 0.5-4 mm. longi. Hypanthium cum calyce minute puberulum. Fructus subglobosus, ad 9 mm. diam.

Woody vine; branches minutely puberulent at first, terete, drying almost black; nodes not conspicuously enlarged, the internodes elongate. Petioles canaliculate, minutely puberulent, up to 11 mm. long. Leaf blades subcoriaceous or coriaceous, ovate-elliptic, ovate-oblong, or lanceolate, 6 to 12 cm. long, 3 to 5.5 cm. wide, apex subabruptly short acuminate, base rounded and abruptly decurrent, acute, costa and primary veins impressed above, prominent beneath, the primary veins 4 to 6 on each side, branching and anastomosing near the margin, veinlets remote and scarcely evident. Inflorescence axillary, paniculate, up to 10 cm. long, pedunculate, minutely puberulent; bracts sometimes foliaceous; bractlets linear or subulate, puberulent. Pedicels 0.5 to 4 mm. long. Calyx and hypanthium minutely puberulent, the calyx scarcely half as long as the hypanthium, the lobes ciliate. Fruit subglobose, only slightly compressed at maturity, up to 9 mm. in diameter.

BRITISH HONDURAS: Toledo District, Cow Pen, near Monkey River, in hammock in pine ridge, Sept. 2, 1942, *Percy H. Gentle 4115* (type in the University of Michigan Herbarium), woody vine, berries white.

Although closely related to *C. pachyphylla* Wernham, the species differs at once in having minutely puberulent branches, and smaller puberulent hypanthium and calyx. The British Honduran plant is a woody vine, while *C. pachyphylla* is described as being a shrub or small tree.

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Notes on the Nomenclature of *Carya* Nutt.

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Various notes on nomenclature have been recorded by the author while checking the scientific names of the forest trees of the United States, as used in the Forest Service, to conform with the International Rules of Botanical Nomenclature. It is planned to publish these notes, including reasons, where it is necessary to change names, in a few journal articles. The first article contains notes on *Carya* Nutt. (family Juglandaceae), which formerly was known also as *Hicoria* Raf. and which bears the common name Hickory. The revised nomenclature, including such changes in names as are essential, will be embodied in a new Check List to replace the Check List of the Forest Trees of the United States by Sudworth (1927), which is an accepted standard in the Forest Service and the Government Printing Office.

The chief reason for revising the nomenclature is the uniform adoption of the International Rules of Botanical Nomenclature (Briquet, 1935) by the United States Department of Agriculture, as authorized by the Secretary of Agriculture's order of April 30, 1940. The last Check List (Sudworth, 1927) in the main followed the American Code of Nomenclature (Botanical Club, 1907), which formerly was used by many botanists and botanical institutions in this country. There is also a need of much closer agreement with the new edition of Standardized Plant Names (Kelsey and Dayton, 1942), which is also a recognized authority of the Department of Agriculture and the Government Printing Office. Various changes, mostly in English names, have been made in Forest Service nomenclature by several orders of the Chief of the Forest Service. A mimeographed list of Approved Changes in Sudworth's Check List, mainly in English names to conform with the revision of Standardized Plant Names, was issued by the Forest Service (1940) before the publication of the new edition of the latter. It is desirable also to compile in usable form in one publication the results of the many taxonomic investigations on the forest trees of the United States which have been made during the fifteen-year interval since the last Check List, long out of print, appeared.

The original citations of the names of the genera, species, and varieties of the forest trees of the United States have been verified and checked with the International Rules of Botanical Nomenclature (Briquet, 1935). Fortunately, the number of names which must be changed on account of the rules and the trend towards more conservative nomenclature is not large. Very few new names and new combinations must be made. Some of the changes were caused by abandoning the American Code, which did not recognize *nomina conservanda*. Other changes include the results of recent taxonomic monographs and field and herbarium studies.

The difficult genus *Carya* Nutt. is in much need of critical taxonomic study. Though no attempt has been made to monograph the genus, several

points of interest on the nomenclature were discovered when the names were transferred from *Hicoria* to *Carya*. Unfortunately, a few names in use under *Carya* must be changed. Three new combinations and one new name are published here, though they appeared inadvertently as *nomina nuda* in Standardized Plant Names (Kelsey and Dayton, 1942, p. 92).

Carya Nutt. and *Hicoria* Raf.

During the period of years that the two rival codes of botanical nomenclature were in use in the United States, the most important difference from the viewpoint of foresters involved the generic name of the Hickories. The United States Forest Service, following Sudworth (1893; 1897; 1898; 1927), adopted *Hicoria* Raf., the earliest name, while some others, including Sargent after 1907 (1907; 1913; 1918; 1922), used *Carya* Nutt., long established in usage and a *nomen conservandum* under the International Rules (Wettstein, 1906, p. 239). *Carya* Nutt. is the only large genus of trees in the United States which has been adopted as a *nomen conservandum*. Now that the American Code has been abandoned, some of its best features having been incorporated into the International Rules, the Forest Service and other foresters uniformly accept *Carya* Nutt.

As the generic name *Hicoria* Raf. has at last been dropped, it may be of interest to review the history of the two rival generic names of Rafinesque and Nuttall. Rev. Henry E. Muhlenberg probably was not aware of what he was starting when in 1801 he first hinted the generic segregation of the hickories but evaded the issue by leaving it for others to decide. He (1801, p. 387; 1805, pp. 241-242) began his paper on *Juglans*, *Fraxinus*, and *Quercus* in the vicinity of Lancaster, Pennsylvania, as follows:

JUGLANS

I arrange the species growing with us under two divisions; the first, containing the common walnut, exactly corresponds with the characters LINNAEUS has given of *Juglans*; the second, comprehends several species of what the inhabitants call Hickery-trees. In the flowers of the latter I never found more than four square anthers, and I leave it to others to decide whether on this account they ought to be separated into a new genus.

Shortly afterwards, other workers also divided *Juglans* into the two sections of walnuts and hickories, though without scientific names. Britton (1888, p. 280) attributed this separation to Michaux (Fl. Bor.—Amer. 2:192. 1803), and Nuttall (1842, 1:38) gave the credit to Persoon (Synops. Pl. 2:566. 1807). Willdenow (Sp. Pl. ed. 4, 4:457. 1805) distinguished the two groups also.

During its existence as a genus, *Hicoria* was spelled in eight different ways: *Scoria* by Rafinesque (1808), *Hicorius* by Rafinesque (1817), *Hiccorius* by Steudel (Nomencl. Bot. 1:164, 404. 1821), *Hicoria* by Rafinesque (1838), *Scorias* by Endlicher (Gen. Pl. 1126. 1840), *Hickoria* by Nuttall (1842), *Hickorea* by Le Conte (1853), and *Hicorias* by Bentham and Hooker (Gen. Pl. 3:398. 1880). Six of these spellings were recorded by Dalla Torre and Harms (Gen. Siphon. 117. 1900). Of the eight spellings, *Hicorius* apparently is the correct one under present rules.

The generic segregation of the hickories began in 1808 with a brief note by Rafinesque (1808), which listed a number of new genera he planned to publish in "two intended works on botany" that never were issued. He wrote (1808, pp. 351, 352):

Besides a variety of others, I shall re-establish in this work about thirty new genusses, from plants already mentioned in authors; but which I have, by observation found to disagree sufficiently from the genusses where they were placed, to oblige me to separate them for the advantage of the science. These will be...

Scoria (tomentosa, mucronata, alba, pyriformis, globosa, &c.) *Juglans* alba L. tormentosa, mucronata, Michx. &c. the hiccory.

A French translation of Rafinesque's article was published the next year by Desvaux (Jour. de Bot. 2:170. 1809; not seen) with the spelling *Scoria* retained but the word "tormentosa" under *Juglans* corrected to "tomentosa."

According to present rules (Briquet, 1935, Articles 41 and 42), *Scoria* (apparently a typographical error changed by Rafinesque himself to *Hicorius* in 1817 and to *Hicoria* in 1838) would not be considered validly published, as a genus is not validated merely by mention of the included species. The name could be rejected also as a *nomen provisorium* under Article 37 ter. Furthermore, correction of the spelling of the first letter and first syllable to *Hicoria* might be questioned under Article 70, Note 2 bis. If Rafinesque had actually published the intended work with a description of this genus, there would have been justification for taking up the name.

The genus *Hicorius* was properly though briefly published by Rafinesque (1817) in his *Florula Ludoviciana*. However, contemporary botanists had sufficient reason for ignoring even a good genus appearing in that book of questionable scientific value. As Gray (1841, pp. 231, 233) later explained, Rafinesque took Robin's *Flore Louisiane*, containing popular notes made from living plants, and without seeing specimens or traveling within a thousand miles of Louisiana, established 30 new genera and 196 new species. Gray added (p. 233) that the only result was to burden botany with a list of species always unknown and concluded: "There can, we think, be but one opinion as to the consideration which is due to these new genera and species: they must be regarded as fictitious, and unworthy of the slightest notice."

No mention was made of the earlier spelling *Scoria* or of the typographical error, when Rafinesque (1817, p. 109) technically published his genus *Hicorius* in that odd work with the following brief statement:

.... My genus *Hicorius*, long ago proposed, contains all the species of *Juglans* which have trifid male flowers (instead of six cleft) generally tetrandrous, and fruits with angular and quadrifid shells.

With the generic description were two species of *Hicorius*, the new combination *Hicorius amara* (Michx. f.) Raf. and *Hicorius integrifolia* Raf., a new species. The name *Hicorius* appeared also on pages 9, 142, and 161. In the appendix, p. 161, he listed seven species of hickories all under *Juglans*, without transferring them to *Hicorius*. However, he wrote: "Those names are Michaux's. All the hickories belong to the genus *Hicorius*; . . ." *Hicorius* was listed on page 126 under "Index of old genera" and not under the new genera.

The next year, Nuttall (1818, 2:220-222) proposed for the hickories his genus *Carya*, a Greek word meaning "nut," which Nuttall stated was the name Greeks applied to the walnut tree, *Juglans regia*. There was an English description of two paragraphs, and nine species, including one new species, and one new variety. Rafinesque's *Hicorius* was not mentioned, and the only reference to previous authors was the very brief citation for the new genus: "*CARYA. †JUGLANS species, L. Willd. (Hickory)." Six of the nine species were listed without description and will be referred to in another part of this article.

In his review of Nuttall's work, Rafinesque (1819a) protested in three places against *Carya*. Under the discussion of Nuttall's new genera he wrote (p. 187): "... We should have seen with more satisfaction an apology for the adoption of unwarrantable bad names, or for the old genera given as new. We shall indicate these erroneous names, or genera, by this mark ! or !!" Near the bottom of the list was "*Carya* ! ! !"

On page 188 Rafinesque remarked: "We find besides these a previous genus *Ensenia* different from the second *Ensenia* of Nuttall, a genus *Hicorius* identical with the *Carya* of Nuttall, &c.!" Then on page 195 he added: "*Carya*, N., was named *Hicorius*, by Raf. in 1808; in 1817, no notice is taken of it. *Carya* is inadmissible, being a radical Greek name, contained in *Caryocar*, *Eucarya*, *Tricharia*, &c."

Rafinesque (1819b, p. 260) in a French review of Nuttall's work, wrote: "*Hicorius*, Raf. Obs., Fl. Ludov., 1817, a été changé sans cause en *Carya* N., nom postérieur radical et très-mauvais."

One of the first authors to mention Rafinesque's and Nuttall's rival names, Steudel (Nomen. Bot. 1:164, 404. 1821) regarded both as synonyms of *Juglans* and, incidentally, used his own new spelling, *Hiccorius*.

Rafinesque discussed this genus in apparently only one other publication (1838, pp. 65-67) and then with his third spelling, *Hicoria*. Here he distinguished also four subgenera and three new species. He wrote:

HICORIA OR HICKORY-TREES

286. HICORIA Raf. 1808. *Carya* Nuttall 1818 &c. As early as 1804 I proposed to separate the Hickories from Walnuts, to which Muhlenberg objected. I did so in 1808 in my remarks on Michaux flora, and again in 1817 in my *Florula Ludoviciana*, giving the almost Grecian name of *Hicoria*; yet Nuttall changed it in 1818 (without mentioning my labor) into *Carya* which merely means *Nut*! and is as bad a name as that of *Nux* given by Adanson to *Juglans*, since it is the root of many other names *Caryocar*, *Caryota*, *Eucarya*, *Araucaria*, *Matricaria*, *Eleocarya* &c. some botanists have however adopted this bad name; but is hoped will have no objection to my previous modification of it, when they may know of my previous claim—although this G. is well distinguished from *Juglans* by the fruit not a drupe, but a 4valve capsule, yet there are many anomalies in the flowers not yet well stated, and that I mean partly to indicate, as well as some new species.

In a later summary of his *Alsographia Americana*, from which the quotation above is taken, Rafinesque (1840, pp. 48-49) mentioned among his "monographs" the one "—of Hickory trees or *Hicoria* Raf. 1808, 4 subg. and 4 new sp."

Nuttall's reply came in his North American Sylva (1842-1849, 1:38. 1842) published after Rafinesque's death in 1840. In a footnote he repeated that *Carya* was from "the ancient Greek name of the Walnut." Spelling Rafinesque's name in still a different way, *Hickoria*, he added:

Hickory is an Indian name for some of the species of this genus; one of them was known to the Indians by the name of *Pecan* or *Pakan*; Rafinesque applied the barbarous name *Hickoria* to this genus, without describing or limiting it; in so doing he has no higher claims for the adoption of the name than our woodsmen and the aborigines.

Like many of Rafinesque's genera, *Hicoria* was ignored by his contemporaries. Rafinesque's botanical writings, including the *Florula Ludoviciana* referred to above, were evaluated shortly after his death by Gray (1841). In quoting the list of genera proposed in Rafinesque's (1808) article, he noted that nearly all of these were admitted by botanists, although mostly under different names. He added (1841, p. 228) after *Scoria*, "[doubtless misprint for *Hicoria*,]" and remarked that, "*Hicoria*, or *Hicorius*, was ten years later called *Carya* by Nuttall."

Though he never did take up *Hicoria* but always used *Carya*, Gray (1841, p. 234) wrote in another place:

It is indeed a subject of regret, that the courtesy which prevails among the botanists of the present day, (who are careful to adopt the names proposed by those who even suggest a new genus,) was not more usual with us some twenty years ago. Many of Rafinesque's names should have been adopted; some as matter of courtesy, and others in accordance with strict rule. But it must be remembered, that the rule of priority in publication was not then universally recognized among botanists, at least as in present practice, (the prevalence of which is chiefly to be ascribed to the influence of De Candolle;) the older name being preferred *caeteris paribus*, but not otherwise.

Apparently only one additional new name was made in *Hicoria* until Britton revived the genus in 1888. LeConte (1853, p. 402) used still another variation in spelling when he described a new species of the "pacane nut," *Hickorea texana*. In adopting Rafinesque's generic name, Le Conte expalined:

I have adopted Mr. Rafinesque's name, *Hickorea*, for the genus, in preference to Mr. Nuttall's *Carya*, on the ground of priority. Whatever may have been the errors or aberrations of Rafinesque, Nuttall was not justified in changing a name proposed by the former, years before any publication of his own.

In reviewing the catalog of the Torrey Botanical Club (1888, p. 49), in which Britton and others made new combinations in *Carya* on the basis of priority of specific epithets, Greene (1888, p. 188) suggested that the time was also opportune, though late, for restoring Rafinesque's genera in botany as zoologists had done. He wrote: "In botany, *Hicorius*, Fl. Ludov. 109 (1817), conclusively antedates *Carya*, Nutt. Gen. ii. 220 (1818), and, being the correctly Latinized aboriginal name of these American trees, is altogether unobjectionable."

James Britten (1888, pp. 260-261) did not approve these tendencies in American botanical nomenclature, as shown by the catalog by the Torrey Botanical Club (1888) and by Greene's articles. In ridiculing the "new and particularly irritating synonymy" of the specific names of *Carya* and Greene's proposal for restoring *Hicorius*, Britten suggested that *Scoria* Raf., the oldest

name, should be taken up instead. He observed two more misspellings, *Hicorias* and *Scorias*. Bentham and Hooker (Gen. Pl. 3:398. 1880) had cited as synonyms of *Carya*, "*Hicorias et Scorias, Rafn. ex Endl.*" However, as Britten noted, only the latter misspelling, *Scorias*, originated with Endlicher (Gen. Pl. 1126. 1840). Durand (Index Gen. Phaner. 379. 1888) and Engler (Engler and Prantl, Natürl. Pflanzenfam. 3 (1):25. 1889), following Bentham and Hooker, listed the spellings *Hicorias* and *Scorias* also as synonyms of *Carya*.

Before the end of the same year, Britton (1888), in his reform movement to restore priority in botanical nomenclature, followed Greene's suggestion, summarized the history of the genus, and did reestablish Rafinesque's generic name with the spelling *Hicoria*. He recognized ten species and one variety, with keys, synonymy, and notes. Three of these species, *Hicoria alba*, *H. aquatica*, and *H. sulcata* had been listed by Rafinesque (1838, p. 66) but with the only citation as "*Carya* Nuttall 1818 &c" under the genus.

Sargent (1889) took up the genus with the spelling *Hicorius*, stating that *Scoria* Raf. was not validly published because no characters were given. In reviewing this paper, Britton (1889, p. 311) remarked: "I have elsewhere shown that the older spelling was *Hicoria*." Sargent changed to the spelling *Hicoria* in his *Silva* (1891-1902, 7:131. 1895) and his *Manual* (1905, p. 131).

Following James Britten's more or less humorous suggestion that *Scoria* should be adopted, Kuntze (1891-93, 2:637-638. 1891) in his radical changes in nomenclature seriously accepted *Scoria* Raf. as the valid name and made one new combination in it. He noted that the spelling *Scoria* was used twice, in 1808 and 1809, and was not changed until 1817. When he reviewed Kuntze's work, Britton (1892, p. 63) wrote: "I have already shown that *Scoria* is a misprint for *Hicoria*. . . Dr. Kuntze does not seem to have seen my paper." MacMillan (1892, pp. 177-178), the only American to follow Kuntze, made two new combinations in *Scoria*.

Under the International Rules of Botanical Nomenclature adopted in 1905 by the International Botanical Congress at Vienna (Wettstein, 1906, p. 239), *Carya* Nutt. was included in the list of *nomina conservanda* and *Scoria*, *Hicorius*, and *Hicoria* of Rafinesque all listed as *nomina rejicienda*. From that date until about 1935, the two rival codes and names were in use. Sargent (1913; 1918; 1922) adopted *Carya* in his later taxonomic treatments of the genus.

Nuttall's Specific Names in *Carya*

In proposing his new genus *Carya* without mentioning Rafinesque's *Hicorius*, Nuttall (1818, 2:220) made the transfers irregularly and without proper citation of the specific names and authors under *Juglans*, as noted above. Britton (1888, p. 280) commented upon Nuttall's publication of the new names in *Carya*, as follows:

Quite ignoring Rafinesque, he [Nuttall] publishes the genus as containing species of *Juglans* of Linnaeus and Willdenow, gives a list of nine species without their equivalents

and with descriptions of three only, yet, inasmuch as many of his specimens are preserved, he is generally cited as author of the binomials.

The six new names published without descriptions or citations are: *Carya alba*, *C. amara*, *C. aquatica*, *C. myristicaeformis*, *C. olivaeformis*, and *C. porcina*. Under a broad interpretation of the International Rules and with proper consideration for the customs of the time, Nuttall's new names in *Carya* could be accepted as new combinations based upon the corresponding specific names under *Juglans* in the works of Linnaeus and Willdenow. However, Linnaeus used only one of these names, *Juglans alba* L. (Sp. Pl. 997. 1753), and Willdenow (Sp. Pl., ed. 4, 4:457. 1805) had two, *Juglans alba* and *J. olivaeformis*. The remaining four names were published as new species by F. A. Michaux (Hist. Arbr. For. Amér. Sept. 1:177, 182, 206, 211. 1810). As Nuttall did not cite Michaux's name or book or the specific names under *Juglans*, the corresponding names of Nuttall must be interpreted under Article 44 as *nomina nuda*, and the combinations were validated by later authors. As three of the six epithets are synonyms in *Juglans* and need not be considered further, only the remaining three, *Carya aquatica*, *C. myristicaeformis*, and *C. alba*, will be discussed below.

***Carya aquatica* (Michx. f.) Nutt.**

WATER HICKORY

Juglans aquatica Michx. f., Hist. Arbr. For. Amér. Sept. 1: 182, pl. 5. 1810.

Carya aquatica Nutt., Gen. No. Amer. Pl. 2: 222. 1818; *nomen nudum*.

Carya aquatica (Michx. f.) Nutt. ex Ell., Sketch Bot. S.-Car. Ga. 2: 627. 1824.

Hicoria aquatica Raf., Alsogr. Amer. 66. 1838; *nomen*, and perhaps irregular new combination based upon *Carya aquatica* Nutt.

Hicoria aquatica (Michx. f.) Britton, Torrey Bot. Club Bul. 15: 284. 1888.

***Carya myristicaeformis* (Michx. f.) Nutt.**

NUTMEG HICKORY

Juglans myristicaeformis Michx. f., Hist. Arbr. For. Amér. Sept. 1:211, pl. 10. 1810.

Carya myristicaeformis Nutt., Gen. No. Amer. Pl. 2: 222. 1818; *nomen nudum*.

Carya myristicaeformis (Michx. f.) Nutt. ex Ell., Sketch Bot. S.-Car. Ga. 2: 628. 1824.

Hicoria myristicaeformis (Michx. f.) Britton, Torrey Bot. Club Bul. 15: 284. 1888.

The combinations *Carya aquatica* and *Carya myristicaeformis* were validated by Elliott (Sketch Bot. S.-Car. Ga. 2:627, 628. 1824), who, as apparently the next author to use them, published Latin and English descriptions and cited the volumes and pages where the species were listed in the works of F. A. Michaux, Pursh, and Nuttall. However, Elliott did not mention the corresponding names under *Juglans*.

Additional field studies are needed to determine whether *Carya fernowiana* Sudw. (in Sudw. and Fernow, Trees of Washington, D. C. 6. 1891), Fernow Hickory, is specifically distinct from *Carya myristicaeformis* (Michx. f.) Nutt. and, if so, the geographic distribution and relationships of the two species. The former name was published simultaneously under both genera, in a list as *Carya* and in a footnote with description as *Hicoria fernowiana* Sudw. (in Sudw. and Fernow, Trees of Washington, D. C. 6. 1891). Though under Article 37 ter it is not clear which name was accepted, both names were validated by the Gray Herbarium Card-Index (Issue 133), and *Carya fernowiana* Sudw. was further validated later by Durand and Jackson (Index Kew. Sup. 1:84).

Carya fernowiana Sudw. was described from a single cultivated tree, "supposed to have been brought from the South," and planted in Washington, D. C. It has generally been regarded as a synonym of *Carya myristicaeformis* (Michx. f.) Nutt., though Sudworth (1897, p. 112) afterwards observed that the form upon which his new species was founded was very different in cultivation from the true *Carya myristicaeformis* as growing wild. Dayton (1937) located the type tree of Sudworth's species, still growing in the Mall in Washington, D. C. He concluded that *Carya fernowiana* is not a synonym and suggested that "*Carya myristicaeformis*" of late dendrological literature may be in part *Carya fernowiana* Sudw.

Carya tomentosa Nutt.

MOCKERNUT HICKORY

?*Juglans tomentosa* Lam., Encycl. Méth. Bot. 4:504. 1798 (?).

Juglans tomentosa Michx. f., Hist. Arbr. For. Amér. Sept. 1: 184, pl. 6. 1810.

Carya tomentosa Nutt., Gen. No. Amer. Pl. 2: 221. 1818.

Hicoria tomentosa Raf., Alsogr. Amer. 66. 1838; nomen, and perhaps irregular new combination based upon *Carya tomentosa* Nutt.

This species was formerly known as "*Carya alba* (L.) K. Koch," but the name *Carya tomentosa* Nutt. has been adopted for the Mockernut Hickory in several recent works, including Palmer and Steyermark (Mo. Bot. Gard. Ann. 22:515. 1935), Deam (Fl. Ind. 370. 1940), and Rehder (Man. Cult. Trees Shrubs, ed. 2, 123. 1940).

It appeared on first checking that *Carya alba* (L.) Nutt. should be the proper name for the Mockernut Hickory. *Carya alba* Nutt. (Gen. N. Amer. Pl. 2:221. 1818) is either an irregular new combination based upon *Juglans alba* of Linnaeus and of Willdenow, the authors cited under the genus, or is a *nomen nudum*. If Nuttall's publication of the name should be passed over as a *nomen nudum*, the combination *Carya alba* (L.) Nutt. might be regarded under Article 54 as published by Elliott (Sketch Bot. S.-Car. Ga. 2:624. 1824), who had *Carya alba* "Lin" and cited "*Juglans Alba*, Lin. Sp. pl. ed. prior, p. 14-15," the page reference in the third edition, 1764. Elliott's description and other citations were *Juglans alba* Michx., now known as *Carya ovata* (Mill.) K. Koch. However, under Article 54 the combination would be associated with Linnaeus' species rather than with Elliott's description. One of the first authors to mention *Carya alba* Nutt., Steudel (Nomencl. Bot. 1:442. 1821), listed it with a question mark as a synonym of *Juglans alba* L. (non Michx.).

Professor Alfred Rehder, of the Arnold Arboretum of Harvard University, who has kindly examined this manuscript, has called to my attention that *Juglans alba* L. (Sp. Pl. 997. 1753) is apparently a mixture and belongs only partly to the Mockernut Hickory, that the figures cited there are not convincing as to the species they represent, and that Linnaeus' statement "*foliolis saepius quinis*" points to *Carya ovata* and excludes the Mockernut Hickory. Thus, *Juglans alba* L., the only species of hickory in the Species Plantarum (1753) might be rejected as apparently a mixture or *nomen confusum* under Article 64.

Carya tomentosa Nutt. was published with a brief description without mention of previous authors and stands as a new species rather than a new combination based upon the earlier names of Lamarck or F. A. Michaux. It is the same as *Juglans tomentosa* Michx. f. (Hist. Arbr. For. Amér. Sept. 1:184, pl. 6. 1810) but may not be identical with the earlier *Juglans tomentosa* Lam. (Encycl. Méth. Bot. 4:504 [?]), which was not cited by F. A. Michaux or by Nuttall.

Miscellaneous Notes on *Carya*

Miscellaneous notes on the nomenclature of seven species, varieties, and hybrids of *Carya* follow.

Carya illinoensis (Wangenh.) K. Koch

PECAN

Juglans pecan Marsh., Arbustr. Amer. 69. 1785; *nomen nudum*.

Juglans illinoensis Wangenh., Beitr. Deutsch. Holzger. Forstwiss. Anpflanz. Nordamer.

Holz. 54, pl. 18, fig. 43. 1787; excluding fruit.

Juglans angustifolia Ait., Hort. Kew. 3: 361. 1789.

Carya angustifolia (Ait.) Sweet, Hort. Brit. 97. 1827.

Carya illinoensis (Wangenh.) K. Koch, Dendr. 1:593. 1869.

Hicoria pecan (Marsh.) Britton, Torrey Bot. Club Bul. 15:282. 1888.

Carya pecan (Marsh.) Engl. and Graebn., Berlin Bot. Gart. u. Mus. Notizbl. App. 9: 19. 1902; non *Carya pecan* (Walt.) Nutt., No. Amer. Sylva 1: 41. 1842.

When the names were being verified, it was discovered that the familiar and appropriate name, *Carya pecan* (Marsh.) Engl. and Graebn. must be rejected for the Pecan under Articles 37 and 61, because it was based upon *Juglans pecan* Marsh., almost a *nomen nudum*, and because of an overlooked earlier homonym, *Carya pecan* (Walt.) Nutt., not in the Index Kewensis. In response to a request concerning the proper name for this species, Rehder (1941, pp. 571-572) has taken up the next oldest name, *Carya illinoensis* (Wangenh.) K. Koch and has discussed the nomenclature with detailed synonymy.

Modern use of the specific epithet *pecan* dates from Britton's (1888, p. 282) acceptance of it, based upon Marshall's (1785, p. 60) inadequate description, quoted in full:

JUGLANS pecan. *The Pecan, or Illinois Hickery.*

This tree is said to grow plenty in the neighborhood of the Illinois river, and other parts to the westward. The young plants raised from these nuts, much resemble our young Pig-nut Hickerys. The nuts are small and thin shelled.

Juglans illinoensis Wangenh., the next oldest name, is not without objections because the fruit was described as reniform and the drawings of the fruit resembled a large bean seed except with the attachment near one end. If the full description and natural size drawing of a leaf did not identify the species much more accurately than many early, brief descriptions, possibly the name might be rejected as a *nomen confusum* derived from two entirely discordant elements (Article 64). The original spelling was changed by Koch as a correction of a typographical error permitted by Article 70. If Wangenheim's name should be rejected, the next available name is *Carya angustifolia* (Ait.) Sweet. As Rehder has noted, the name *Carya illinoensis* (Wangenh.) K. Koch was

adopted by Robinson and Fernald (Gray's New Man. Bot., ed. 7, 331. 1908) in their standard work and is already in use.

***Carya texana* Buckl.**

BLACK HICKORY

Carya texana Buckl., Acad. Nat. Sci. Phila. Proc. 1860 [v. 12]: 444. 1860; non *Carya texana* C. DC., Ann. Sci. Nat., Bot., sér. 4, 18: 33. 1862; non "*Carya texana*" of Sarg. and other authors; non *Hickorea texana* Le Conte, Acad. Nat. Sci. Phila. Proc. 6: 402, illus. 1853.

Carya buckleyi Durand, Acad. Nat. Sci. Phila. Proc. 1860 [v. 12]: 547. 1861.

Hicoria buckleyi (Durand) Ashe, Elisha Mitchell Sci. Soc. Jour. 34: 131. 1918.

It is regretted that the names in use for a species and a hybrid must be changed to conform to the International Rules, especially as the epithet of the latter must be restored to the former. The epithets in use are correct under *Hicoria* but not under *Carya*, and it is unfortunate that the incorrect application was not detected when the names were revived some years ago. For the species familiarly known as *Carya buckleyi* Durand (1861), the prior name *Carya texana* Buckl. (1860) must be adopted. The hybrid between *Carya aquatica* and *Carya illinoensis*, known as " \times *Carya texana* (Le Conte) C. DC." (1862) of authors, must be given a new name.

The new species *Carya texana* Buckley was published in the Proceedings of the Academy of Natural Sciences of Philadelphia for October 1860. The name was changed to *Carya buckleyi* Durand in the Proceedings for December 1860 (minutes of the meeting December 4) because of the earlier and different *Hickorea texana* Le Conte, though the latter had not been transferred to *Carya*. Under Article 54, the epithet *texana* must not be re-established when Le Conte's name is transferred to *Carya* because the resulting binary name would be a later homonym of *Carya texana* Buckl. Thus, *Carya texana* Buckl. stands under Article 16 as the earliest name, and *Carya buckleyi* Durand must be rejected under Article 60 (1) as superfluous when published.

Sargent (1902-1913, 2: 205-206. 1913) in taking up this species under the name *Carya buckleyi* Durand apparently was misled by the name *Hickorea texana* Le Conte when he wrote: "... the name *Carya texana* had been used by another author for an entirely different species before Buckley applied it to this tree; ..."

It is necessary to transfer Sargent's two varieties of *Carya buckleyi* Durand to *Carya texana* Buckl. (Acad. Nat. Sci. Phila. Proc. 1860 [v. 12]: 547. 1861) as new combinations. Their detailed synonymy is given below:

***Carya texana* Buckl. var. *arkansana* (Sarg.) Little, comb. nov.**

ARKANSAS BLACK HICKORY

Carya arkansana Sarg., Trees and Shrubs 2: 203, pl., 181. 1913.

Carya buckleyi var. *arkansana* (Sarg.) Sarg., Bot. Gaz. 66: 249. 1918.

Hickoria arkansana (Sarg.) Ashe, Elisha Mitchell Sci. Soc. Jour. 34: 132. 1918.

Hicoria pallida [var.] *arkansana* (Sarg.) Ashe, Elisha Mitchell Sci. Soc. Jour. 34: 132. 1918.

Hicoria buckleyi arkansana (Sarg.) Ashe, Charleston Mus. Quar. 1 (2): 29. 1925.

Carya texana Buckl. var. *villosa* (Sarg.) Little, comb. nov.

VALLEY BLACK HICKORY

Hicoria glabra var. *villosa* Sarg., Silva No. Amer. 7:167, pl. 355. 1895.

Hicoria odorata var. *villosa* (Sarg.) Ashe, Notes on Hickories U. S. 1. 1896.

Hicoria villosa (Sarg.) Ashe, Torrey Bot. Club Bul. 24:481. 1897.

Carya villosa Schneid., Illus. Handb. Laubholz. 1: 803. 1906.

Carya glabra var. *villosa* Robins., Rhodora 10: 32. 1908.

Carya buckleyi var. *villosa* (Sarg.) Sarg., Bot. Gaz. 66: 251. 1918 (Sept. 16).

Hicoria pallida [var.] *villosa* (Sarg.) Ashe, Elisha Mitchell Sci. Soc. Jour. 34: 132. 1918 (Oct. ?).

Hicoria buckleyi villosa (Sarg.) Ashe, Charleston Mus. Quart. 1(2): 29. 1925.

× *Carya lecontei* Little, nom. nov.

BITTER PECAN

Carya aquatica (Michx. f.) Nutt. × *Carya illinoensis* (Wangenh.) K. Koch.

?*Hicoria texana* Le Conte, Acad. Nat. Sci. Phila. Proc. 6: 402, illus. 1853; as "*Hickorea*."

Carya texana C. DC., Ann. Sci. Nat., Bot. sér. 4, 18: 33. 1862; non *Carya texana* Buckl., Acad. Nat. Sci. Phila. Proc. 1860 [v. 12]: 444. 1860.

"*Hicoria texan.* (Le Conte);" Sarg., Silva No. Amer. 14: 43, pl. 719. 1902.

"*Carya texana* Leconte"; Sarg., Trees and Shrubs 2: 206. 1913; *nomen nudum*.

"*Carya texana* Schn." Sarg., Man. Trees No. Amer., ed. 2, 179. 1922.

"*Carya texana* (Le Conte) C. DC. (*C. aquatica* × *C. pecan*)"; Palmer, Arnold Arboretum Jour. 18: 133. 1937.

Le Conte (1853) described *Hickorea texana* as "a new species of the *Pacane* Nut," which he found cultivated in Georgia but which was a native of Texas. I was unable to find a specimen of this at the Academy of Natural Sciences of Philadelphia, which has Le Conte's herbarium.

Casimir de Candolle (1862, p. 33) described *Carya texana* as a new species based upon a specimen collected in east Texas by Charles Wright in 1848-1849. He (p. 37) included it with the species too little known to be placed in the enumeration of species and later treated it similarly as not satisfactorily known. (C. DC. in A. DC., Prodr. 16(2):145. 1864). As there was no mention of *Hickorea texana* Le Conte, the name *Carya texana* C. DC. cannot be interpreted as a new combination. It is doubtful whether the two species are the same. In his treatment of the genus *Hicoria*, Britton (1888) mentioned *H. texana* Le Conte in a note after *Hicoria pecan*, expressing doubt that the former could be referred to the latter but noting that he had found no specimens. At the end of the list he added that he was entirely unacquainted with *Carya texana* C. DC.

Sargent (1891-1902, 14:43, pl. 719. 1902) took up *Hicoria texana* Le Conte as a species and listed *Carya texana* C. DC. as a synonym. Later he (Sargent, 1902-13, 2:206. 1913) used the name "*Carya texana*, Leconte." Afterwards he had "*Carya texana* C. DC." (Sargent, 1918, p. 231) and "*Carya texana* Schn." (Sargent, 1922, p. 179).

More than fifty years ago, Mohr (1889) observed that pecan trees readily hybridized in the forests and in cultivation and that the hybrids yielded unsightly and unpalatable fruit. He reported that crosses between the pecan and *Carya aquatica* were frequently found. Trelease (1896, p. 34) suggested

that *Hickorea texana* Le Conte seemed to be a hybrid, similar to hybrids between *Hicoria pecan* and *Hicoria minima*.

Palmer (1937, pp. 133-135) more recently submitted evidence to show that "the bitter pecan, *Carya texana* (Le Conte) C. DC., is a hybrid between *Carya aquatica* and *C. pecan* . . ." Unfortunately, as discussed above, the epithet *texana* cannot be used, and the hybrid thus is without a name. It seems appropriate to name it \times *Carya lecontei*, in honor of Major John Eaton Le Conte (1784-1860), the American naturalist who described in 1853 a species of pecan which may have been the same or which, since it was in cultivation, may have been a variation of *Carya illinoensis* with large, edible nuts instead of bitter.

\times *Carya lecontei* Little, nom. nov., is to be associated with the detailed, previously published description of "*Hicoria texana* Le Conte" by Sargent (Silva No. Amer. 14:43, pl. 719. 1902). Owing to the uncertainty of the identity of *Hickorea texana* Le Conte and *Carya texana* C. DC., in the absence of specimens, it is desirable to name a type specimen for \times *Carya lecontei*. As Sargent (p. 44) stated that B. F. Bush rediscovered this hickory at Columbia, Texas, in 1899, it is appropriate to designate the following as the type: B. F. Bush No. 105, April 22, 1900. Columbia, Texas (U. S. National Herbarium No. 386,421). Isotype seen at New York Botanical Garden.

\times *Carya ludoviciana* (Ashe) Little, comb. nov. LOUISIANA HICKORY

\times *Hicoria ludoviciana* Ashe, Torrey Bot. Club Bul. 54: 582. 1927.

Carya aquatica (Michx. f.) Nutt. \times *Carya texana* var. *arkansana* (Sarg.) Little.

\times *Hicoria ludoviciana* Ashe was described as a hybrid between *Hicoria aquatica* (Michx.) Britton and *Hicoria buckleyi* var. *arkansana* (Sarg.) Ashe. With the changes in nomenclature, the supposed parents now bear the names *Carya aquatica* (Michx. f.) Nutt. and *Carya texana* var. *arkansana* (Sarg.) Little. Two herbarium specimens of \times *Hicoria ludoviciana* Ashe from the type tree (Caroline Dormon, near Chestnut, Natchitoches Parish, La., Oct. 10, 1926) were kindly lent for study by Dr. W. C. Coker, of the University of North Carolina, where W. W. Ashe's herbarium is located. Ashe noted that this hickory had the foliage, buds, bark, and general aspect of *H. buckleyi*, but resembled the other supposed parent in certain fruit characters. It is possible that additional field study may show this hickory to be an extreme variation of *Carya texana* var. *arkansana*, rather than a hybrid.

Carya glabra (Mill.) Sweet var. *megacarpa* (Sarg.) Sarg.

COAST PIGNUT HICKORY

Carya megacarpa Sarg., Trees and Shrubs 2: 201, pl. 180. 1913.

Carya glabra var. *megacarpa* (Sarg.) Sarg., Bot. Gaz. 66: 244. 1918.

? *Hicoria ashei* Sudw., Amer. Forests and Forest Life 30:334. 1924.

Hicoria austrina Small, Man. Southeast. Flora 406, 1504. 1933.

The place of publication of *Hicoria ashei* Sudw. was cited incorrectly by both the Gray Herbarium Card-Index (Issue 130) and Hill (Index Kew. Sup. 8:1933) as Sudworth (Check List Forest Trees U. S. 57. 1927). There

the name appeared without description or citation but with range stated as Florida, Georgia, and Alabama. Dr. W. C. Coker, of the University of North Carolina, kindly sent for study authentic herbarium specimens of this hickory but without fruit, collected by W. W. Ashe. Additional field study is needed to determine whether this hickory merits recognition and formal transfer of the name to *Carya*. For the present, it may be included tentatively under *Carya glabra* var. *megacarpa* (Sarg.) Sarg., from which it may not be distinct.

Hicoria austrina Small, of Florida, perhaps the most recently described species of the genus in the United States, is a segregate from *Carya glabra* var. *megacarpa* (Sarg.) Sarg. As an examination of the type specimen (Small, Britton, and De Winkeler No. 9191, 5 mi. S. of Daytona, Fla., Nov. 30, 1919) at the New York Botanical Garden shows no significant differences, it seems best under conservative nomenclature to reduce *Hicoria austrina* Small to synonymy.

Summary

1. These notes on the nomenclature of *Carya* Nutt. (formerly *Hicoria* Raf. under the American Code), family Juglandaceae and common name Hickory, were recorded by the author in checking the scientific names of the forest trees of the United States to conform with the International Rules of Botanical Nomenclature. Three new combinations and one new name in *Carya* are published here.

2. The history of the two rival genera, *Carya* Nuttall (1818), *nomen conservandum*, and *Hicoria* Rafinesque (1817), *nomen rejiciendum*, is reviewed. *Hicoria* Raf. had priority of one year but, like many of Rafinesque's genera, was rejected by his contemporaries. Since Britton restored *Hicoria* in 1888, both names have been used and confusion has existed. Now that the American Code has been abandoned, *Carya* is uniformly used.

3. In publishing his new genus *Carya*, Nuttall cited authors briefly and listed some names as *nomina nuda*. The combinations *Carya aquatica* (Michx. f.) Nutt. and *Carya myristicaeformis* (Michx. f.) Nutt. both were validated by Elliott. Field studies are needed to determine whether *Carya fernowiana* Sudw. is specifically distinct from *Carya myristicaeformis*. *Carya tomentosa* Nutt. has been adopted in several recent works for the Mockernut Hickory, formerly known as "*Carya alba* (L.) K. Koch."

4. The scientific name of the Pecan is *Carya illinoensis* (Wangenh.) K. Koch. *Carya pecan* (Marsh.) Engl. and Graebn. must be rejected as it is based upon a *nomen nudum* and is also a later homonym of *Carya pecan* (Walt.) Nutt.

5. The older name, *Carya texana* Buckl. (1860), must be adopted for *Carya buckleyi* Durand (1861). Two new combinations, *Carya texana* Buckl. var. *arkansana* (Sarg.) Little and *Carya texana* Buckl. var. *villosa* (Sarg.) Little, are made.

6. A new name, \times *Carya lecontei* Little, is made for the Bitter Pecan, a hybrid between *Carya aquatica* (Michx. f.) Nutt. and *Carya illinoensis* (Wan-

genh.) K. Koch. It is "*Carya texana*" of Sargent and other authors, a later homonym of uncertain identity.

7. The new combination, \times *Carya ludoviciana* (Ashe) Little, is necessary for \times *Hicoria ludoviciana* Ashe, a hybrid between *Carya aquatica* (Michx. f.) Nutt. and *Carya texana* var. *arkansana* (Sarg.) Little.

8. *Hicoria ashei* Sudw. is tentatively included as a synonym of *Carya glabra* (Mill.) Sweet var. *megacarpa* (Sarg.) Sarg., and *Hicoria austrina* Small is reduced to a synonym of the same variety.

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Phytogeographic Studies of the Mosses of Northern Florida*

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I. Bryogeography

INTRODUCTION

Region to be considered. The part of Florida to be considered here lies between Latitude 29 and 31 North, and is frequently referred to as "continental" Florida, in contrast to "peninsular" Florida. It extends four hundred miles from east to west and is forty to one hundred miles wide from north to south. Most intensive collecting has been in Jackson, Gadsden, Liberty, Franklin, Leon, Wakulla, Jefferson, Madison, Suwanee, and Levy Counties.

Climate of northern Florida. Since climate has a definite effect on vegetation and plant distribution, a brief summary of the climatic conditions in northern Florida is in order here. Proximity to the Atlantic Ocean and the Gulf of Mexico as well as low altitude contribute toward a mild humid climate, although northern Florida lacks completely the semitropical climate of the southern peninsular region. The average annual temperature in northern Florida is 68.6°; July temperatures average 81°, and January, 55°. Although many days during the winter are mild, killing frosts may occur from the early part of November to the last of February, with occasional frost in March or even April. The annual isotherm of 69° runs from Jacksonville to Apalachicola; of 68° from Monticello to Pensacola. The growing season, that is, the time from last spring frost until first autumn frost, is about 280 days. Slightly over half of the annual precipitation, which averages 60.9 inches, comes in June-September, while April and November are usually the driest months. Much of the summer rainfall is due to convectional thunderstorms, since along the central and east gulf coast there are as many as 80-90 days annually with thunder showers. Tropical storms add to the normal rainfall, which occurs on about 114 days of each year. Relative humidity throughout the region is high, especially in late summer when rainfall is more abundant. At Jacksonville, for example, the average humidity at 7:30 A.M. is 86, while at 7:30 P.M. it is 79. (These figures were compiled from statistics of the United States Weather Bureau Section 104, Northern Florida).

Physiography of northern Florida. Two clear-cut topographic units occur in northern Florida, the hill section and the low coastal strip. The altitude

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does not exceed 325 feet in either region, although steep slopes give the impression of altitude. In the vicinity of Gretna in Gadsden County the original plateau (about 300 feet in altitude) has not yet been dissected into hills and valleys (Sellards, 1912).

Differences in surface soils are reflected clearly in the flora. Some soils support rich forests of beech, magnolia, maple, sweet gum, oak, hickory, and tulip poplar. Other soils are covered by stands of pine, black jack and turkey oak. In the flatwoods long-leaf pine is the chief tree, while undergrowth consists of palmetto, wire grass, gallberry, pitcher plants, orchids, etc. The hill section extends to within five or ten miles of the coast, where it abruptly grades into the coastal belt, which consists of flatwoods, swamps, hammocks, tidal marshes, or long stretches of sandy beaches.

Most of the rivers flowing through northern Florida have their origin in southern Alabama and Georgia, and empty into the Gulf of Mexico. The St. Johns, which flows northward and empties into the Atlantic Ocean, is the outstanding exception. It is noteworthy that the three principal streams east of the Apalachicola River and west of the Suwanee, the Ocklocknee, St. Marks, and Aucilla Rivers, flow approximately parallel in a general northeast to southwest direction. Most of their tributaries enter from the north and west, following the general slope of the land toward the southeast (Sellards, 1917). Many of the smaller streams rise in springs. The Apalachicola River, the largest in northern Florida, rises in north Georgia outside the coastal plain. It is bordered by fertile flood plains or high banks which support luxuriant vegetation. Many smaller streams do not amount to more than low swampy places which end blindly in marshes.

East of the Ocklocknee River several large lake basins, such as those of Jackson, Miccosukee, Iamonia, and Lafayette, have been formed by gradual solution of limestone which lies near the surface. The lakes are shallow except for sinkholes which occur in and around the margins. These sinkholes vary in depth from a few feet to as much as seventy-five feet in the one which drains Lake Lafayette. Some gradually fill up with earth as others form. These lakes are very near ground water level, so that during dry seasons they are practically empty and are converted into grazing lands, although water is always found in the deep sinks. A number of deeper lakes occur in the region, such as Lake Hall, Lake Bradford, and Orchard Pond. They average fifteen to twenty-five feet in depth, and while this depth may fluctuate with seasonal rainfall, they always contain some water. West of the Ocklocknee River large lakes are few (Sellards, 1917); sinks fill with water and form small ponds.

Another type of lake is formed by the rapid alluviation of main streams which may dam up more sluggish tributaries at the point where the latter join the main stream. Sellards (1916) and Vernon (1942) have both commented on this condition in describing the formation of the Dead Lakes in Calhoun County. Sellard states:

The valley of the Apalachicola River is being rapidly aggraded by reason of the load of sediment carried by that stream; the valley of the Chipola, on the other hand,

is being built up, much more slowly. The result has been a blocking of the Chipola at its entrance into the Apalachicola by sediment carried by the main stream, thus forming the body of water known as the "Dead Lakes" in Calhoun County.

The lakes have been formed so recently that cypress trees which previously grew in the river swamp still stand, although most of them are dead. The channel of the river may be followed through the lake.

EDAPHIC FACTORS

SAND

Coastal strip. A strip of lowland, five to ten miles wide in most places, which nowhere exceeds a hundred feet in altitude and which is characterized by sandy beaches and dunes of Pleistocene and recent origin, extends from the mouth of the Ocklocknee River westward along the Gulf of Mexico to Mississippi. Vegetation of the dunes and beaches is sparse and largely evergreen, indicating a sterile soil, and consists of grasses, running vines, saw palmetto, and stunted magnolias. *Pinus Elliotti* (slash pine) and/or *Pinus clausa* (spruce pine) grow on the older, stable dunes. The only moss found on the dunes is *Dicranum condensatum*, common all along the Panama City-Long Beach region in Bay County and westward. *Bryum capillare* grows mixed with grasses in damp places protected from wave action but occasionally inundated by salt water.

Palmetto thickets. Vegetation of the salt marshes which occur about the mouths of the rivers and creeks consists of tall stiff grasses, rushes, and occasional groups of *Sabal Palmetto*. The drying action of sea winds prevents the development of many epiphytic mosses. In the palm thickets *Syrhophodon floridanus* is the only species growing more than two or three feet above the ground; it extends up into the crowns of most of the palms, making a heavy growth. *Haplocladium microphyllum*, *Sematophyllum adnatum*, *Bryum capillare*, *Isopterygium micans*, and *Thelia hirtella* cover fallen trees and decaying logs. *Aulacomnium palustre*, *Funaria flavicans*, *Pogonatum brachyphyllum*, and *Polytrichum commune* grow on soil, especially along the moist banks of streams. *Barbula Cruegeri* is common on old oyster shells, and *Tetraplodon australis* occurs on cattle dung. Along the East Coast *Octoblepharum albidum*, a species found abundantly throughout the tropics, is common, but is rare along the northern shores of the Gulf of Mexico.

Pine forests. The surface soils of much of north Florida, with the exception of the red clay hills, consist of loose cream-colored or white, somewhat acid (pH 6-6.5) sand, through which water drains readily. The water of ponds and streams is usually coffee-colored, due to presence of organic matter from the cypress-bay swamps. The vegetation consists characteristically of either pure stands of *Pinus australis* (long-leaf pine) or the scrub, *Quercus marylandica* (black jack) and *Q. Catesbaei* (turkey oak) under which occasional tufts of *Ditrichum pallidum* or *Campylopus gracilicaulis* grow on the loose and sterile soil. As pine bark sloughs off repeatedly, and perhaps because of the accumulation of resin, corticolous bryophytes are rare on pines, and only

those able to grow under very diverse conditions, such as *Isopterygium micans* or *Sematophyllum adnatum*, occur there. *Syrhodon incompletus* was found once on pine, where it was growing thickly in the cracks in the bark.

Black jack. The "scrub oak" (high pine land, Harper, "Geography and Vegetation of Northern Florida") is composed of a comparatively dense scrub-like growth of *Quercus Catesbaei* and *Quercus Margaretta*, not exceeding fifteen feet in height, under open stands of *Pinus australis*. Much of the white sand is exposed by the sparse herbaceous undergrowth of which characteristic elements are *Aristida stricta* (wire grass), *Opuntia Opuntia*, and *Pteridium latiusculum*. Annual burning, usually during dry weather in early spring, has removed most of the organic matter from the soil, so that mosses do not form a conspicuous part of the vegetation. Many of those present are characteristic of dry habitats:

Atrichum Macmillani
Bruchia carolinae
Bryum capillare
Clasmatodon parvulus
Campylopus gracilicaulis
Cryphaea glomerata
Ditrichum pallidum
Entodon seductrix
Funaria calvescens
Funaria serrata

Leucobryum albidum
Leucobryum antillarum
Leucodon julaceus
Isopterygium micans
Sematophyllum adnatum
Thelia hirtella
Thelia Lescurii
Haplocladium microphyllum
Tortella caespitosa
Weisia viridula

Flatwoods. Flatwoods form the predominant vegetation of the coastal lowland strip. As the name implies, the surface is level or nearly so. The water table is usually near the surface so that many shallow depressions develop into ponds filled with cypress or into "tyty" (*Cliftonia* and *Cyrilla*) bays. Although it is generally assumed that soils of flatwoods are acid, in Wakulla County flatwoods where lime rock occurs only fifteen inches or so below the surface have a pH of 7-7.5. As the limestone becomes deeper, the soil becomes more acid, reaching a pH of 4.5 in some places. Differences in depth of limestone give rise, at the extremes, to two general types of flatwoods, the calcareous and acid, although the vegetation of the two types has much the same general aspect. *Pinus australis* is the dominant tree in both. Characteristic of the acid flatwoods are *Aristida stricta* (wire grass), *Serenoa repens* (saw palmetto), *Ilex glabra* (gallberry) and several species of heaths, pitcher plants, and orchids. *Aristida* and *Serenoa* occur in the calcareous flatwoods, as well as *Pityopsis graminifolia* (*Chrysopsis*), *Stillingia sylvatica* and frequently *Atamasco Atamasco* (atamasco lily). As might be expected, the calcareous flatwoods are distinguished principally by the absence of heaths, pitcher plants, gallberry, and other plants usually associated with acid soil conditions. Because of the wetness of the soil, the dense undergrowth, and their bad reputation for snakes, the flatwoods have not been explored very thoroughly. *Sphagnum strictum* grows in mats about the base of palmettos, in many places associated with *Leucobryum albidum*, and *Sphagnum cuspidatum* var. *serrulatum* occurs abundantly in the ditches which drain the flatwoods. Patches of *Bryum capillare*, *Rhynchostegium serrulatum* or *Isopterygium*

micans grow in drier places. In the calcareous flatwoods *Barbula Cruegeri*, *Tortula agraria* and *Thuidium minutulum* grow on limestone outcrops.

CLAY AND LOAMS

Hammocks. In Florida all well drained lands supporting hardwood forests are called "hammocks," whether calcareous or acid, or on high or low ground, in contrast to "swamps," places where water is abundant and gum or cypress predominates. Physiographers recognize several hammock belts: the Middle Florida Hammock Belt, the Gulf Hammock Belt, and the Hard Rock Phosphate Belt (Sellards, 1912), all of which, although underlain by Oligocene limestone, present varying degrees of acidity in their soils. Although limestone has little or no effect on vegetation in dry places, in moister situations many plants characteristic of limestone grow (Harper, 1941). Where limestone is lacking, the presence of mountain laurel and azaleas indicates the sandy and acid nature of the soils in which they occur.

A considerable variety of soils occur, which range from black calcareous to sandy loam or red clay, their color dependent largely on drainage conditions (Henderson, 1939). Not uncommonly soils near streams contain ferruginous nodules, which may have some influence on plant distribution, or at least the chemical and physical conditions of the soil producing them may affect plant development.

Many of the hammocks support climax forest associations, with either a nearly pure stand of beech and magnolia or a mixture of these two species with laurel oak, water oak, tulip poplar, ironwood, holly, and more rarely pine. As usual, the mosses parallel the flowering plants, for many species of mosses occur in the hammocks. Species characteristic of hammocks are:

<i>Jaegerinopsis squarrosa</i>	<i>Macromitrium rhabdocarpum</i>
<i>Homalotheciella fabrofolia</i>	<i>Aulacomnium heterostichum</i>
<i>Homalotheciella subcapillata</i>	<i>Cirriphyllum Boscii</i>
<i>Fissidens Littlei</i>	<i>Syrrophodon parasiticus</i>
<i>Solmsiella Kurzii</i>	<i>S. ligulatus</i>
<i>Ptychomitrium Drummondii</i>	<i>Fabronia Ravenelii</i>
<i>Schwetschkeopsis denticulata</i>	<i>Taxiphyllum planissimum</i>
<i>Schlotheimia Sullivantii</i>	<i>Leskea microcarpa</i>

Lena Stein Ravine. An unusually rich hammock vegetation occurs in a ravine just north of Tallahassee, known locally as "Lena Stein Ravine," which is so unique in its bryophyte flora as to warrant special mention. True *Spagnum* bogs are extremely rare as far south as Florida, yet here an extensive bog occurs. According to Harper (in litt., 1941), "Apparently a sandy stratum overlies some impervious clay, and makes favorable conditions for a perpetual seeping out of water, which favors the growth of *Spagnum* and other mosses." Numerous springs feed the small stream which runs through the ravine, where Dr. A. J. Grout has collected *Sciaromium Lescurii*, *Pogonatum brevicaulis*, *Dicranella Hilariana*, and *Atrichum Macmillani* occur on the moist banks, and *Bruchia Ravenelii* grows abundantly in the grass. Adjacent to the stream the ground is covered with *Rhizogonium spiniforme*, *Sphagnum henryense*,

S. recurvum, and *Polytrichum commune*. *Pinckneya pubens*, which is characteristic of sandy bogs, grows here, as well as *Magnolia glauca*, *Myrica cerifera*, *Acer rubrum*, and the fern *Anchistea virginica*. *Mnium affine*, *M. rostratum*, *M. punctatum*, *Fissidens Bushii*, *F. subcrenatus*, *F. polypodioides*, *F. Ravenelii*, *F. taxifolius*, *Aulacomnium palustre*, and *Thuidium delicatulum* grow on the low ground near the rim of the ravine, usually close to the springs. *Pogonatum brachyphyllum* and *Atrichum Macmillani* are the most typical mosses growing along the rim. On the uplands surrounding the ravine *Pinus Taeda* and *P. echinata*, mixed with *Quercus virginiana*, *Q. nigra*, and *Q. laurifolia* produce an open forest. It is remarkable that a place with so definite a northern aspect should also harbor such species as *Octoblephorum albidum* and *Syrhopodon parasiticus*.

Swamps. Although a luxuriant growth of liverworts covers the lower parts of trees in the cypress and gum swamps, the quantity and variety of mosses are disappointingly poor for such wet habitats. *Fontinalis Sullivantii* grows attached to bushes and bases of trees in stagnant or slow moving water. *Climacium Kindbergii* and *Thuidium delicatulum* grow tangled together on wet soil or on the swollen buttresses or knees of cypress. *Rhizogonium spiniforme* occasionally grows on the wet soils bordering ponds or on the bases of trees in the swamps, but it is more common in the many low wet places of hammock lands. *Sphagnum subsecundum*, *S. recurvum*, *S. macrophyllum*, *S. magellanicum*, *Aulacomnium palustre*, *Polytrichum commune*, *Syrhopodon texanus*, and *Leucobryum albidum* occur commonly in swamps.

River bottoms. Since most of the streams flow only very slightly below the bordering land, they consequently overflow their banks during rainy seasons. The rich alluvial soil is swampy and the air humid, which fosters the luxuriant growth of bryophytes. *Microthamnium diminutivum*, a tropical species reported from only a few stations in Florida, grows on sandy stream banks, characteristically associated with the following species:

<i>Rhynchostegium serrulatum</i>	<i>A. varium</i>
<i>Oxyrrhynchium hians</i>	<i>Ephemerum serratum</i>
<i>O. Rappii</i>	<i>Fissidens cristatus</i>
<i>Campylium chrysophyllum</i>	<i>F. Ravenelii</i>
<i>Breidleria arcuata</i>	<i>F. taxifolius</i>
<i>Leptodictyum riparium</i>	<i>F. viridulus</i>
<i>Amblystegium furatzkanum</i>	<i>F. polypodioides</i>
<i>A. serpens</i>	<i>Thuidium delicatulum</i>

Cyclodictyon varians, a tropical species, grows abundantly on the wet soils of stream banks near Jacksonville but has not yet been collected in the western part of the state.

LIMESTONE

Limestone underlies the whole state of Florida but affects topography only in limited areas since it is usually buried beneath more recent deposits of sands, clays, or marls (Cooke and Mossom, 1929). However, the oldest formation, the Ocala (Eocene), is exposed in parts of peninsular Florida, extending north to Ellaville and west to the Gulf, and again in West Florida

in Jackson County. Its surface is low or gently rolling, with many ponds, sinks, and shallow depressions, although surface streams are few.

In Florida, the Oligocene limestones, which correspond to the Vicksburg group in Mississippi, affect surface topography most. Marianna limestone, which outcrops along the Chipola River in Jackson County, is the oldest Oligocene formation exposed, and consists of a homogeneous, pure limestone, as high as 93-95 percent calcium carbonate. Glendon limestone and Byram marl, formerly thought to extend from a few miles west of the Choctawhatchee River to the Chattahoochee River, are not now recognized in West Florida. Their equivalents are possibly included in the Suwannee limestone of West Florida.

Tampa limestone (Miocene) underlies much of northern Florida, and is exposed especially prominently at Aspalaga and Rock Bluff along the Apalachicola River. Wakulla Springs in Wakulla County rises from a subterranean stream in the Tampa and Suwannee limestones, and the channels of the Wakulla and St. Marks Rivers flow through them.

Although the Alum Bluff Group (Miocene) is represented in peninsular Florida, the best known exposures occur along the east bank of the Apalachicola River in Liberty County, in continental Florida. The Hawthorn, which probably corresponds to the Alum Bluff in Peninsular Florida, is one of the most widely distributed formations in the state, extending from the Apalachicola River to Jacksonville and south to DeSoto County. At Devil's Millhopper, a deep sink in Alachua County, one hundred and fifteen feet of phosphatic rock (Hawthorn formation) are exposed.

There are two distinct types of plants occurring on limestone: those which are typical calciphiles, and those which are apparently not influenced by the alkalinity of the substrate, since they occur in other situations.

European bryogeographers such as Herzog (1926), Amann (1928), and Bizot (1937) have emphasized the effect of the substrate on distribution. Their works contain important references to those species restricted to, or characteristic of, limestone.

Species restricted to limestone in Florida are:

Gyroweisia Barbula
Trichostomum jamaicense
Eucladium verticillatum
Gymnostomum calcareum
Philonotis gracillima
P. sphaericarpa

Desmatodon plinthobius
Tortula agraria
Barbula Cruegeri
Taxiphyllum mariannae
Fissidens manateensis
F. bryoides

Brachythecium acuminatum commonly grows on limestone, especially at the Marianna Caverns, although farther north it ordinarily grows on the trunks of trees. *Brachythecium Roteanum*, *Mnium cuspidatum*, *Haplocladium microphyllum*, *Oxyrrhynchium bians*, and *Amblystegium Juratzkanum* frequently grow on limestone, but grow on other substrata in regions where limestone is absent.

PHYTOGEOGRAPHICAL FACTORS

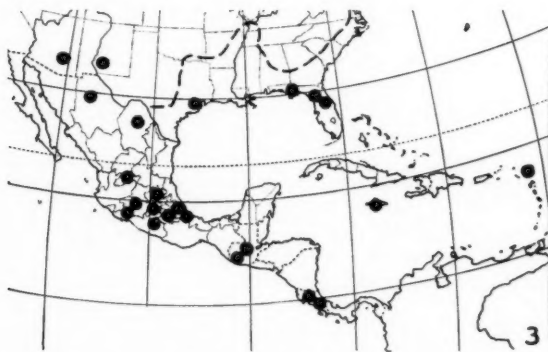
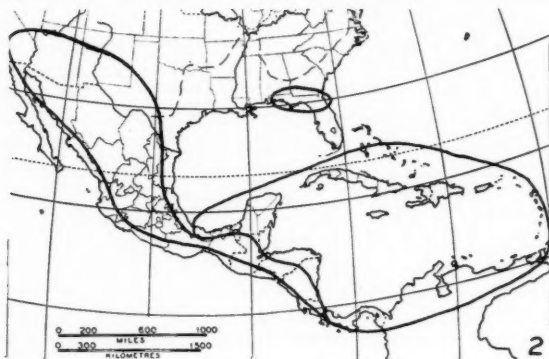
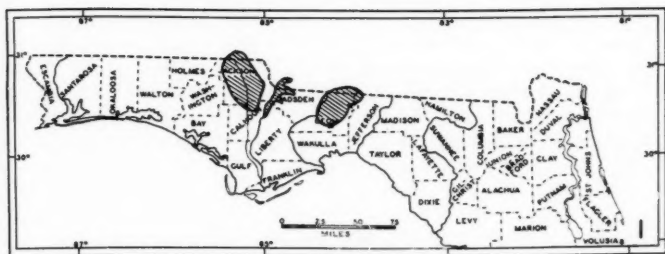
Regions of endemic species. Many northern species apparently reach their southernmost range in three areas in northern Florida covered by rich deciduous forests, completely separated from each other, and surrounded by rolling pine land, scrub forests, or flatwoods. They are (1) Marianna Red Lands, (2) The Apalachicola River Bluffs, and (3) the Tallahassee Red Hills (Map 1). Outcrops at Marianna are Lower Oligocene limestone, whereas along the Apalachicola River Bluffs they are Tampa or Alum Bluff formation (Miocene). No surface exposure of limestone occurs in the Tallahassee Red Hills, although the Hawthorn formation underlies it.

Marianna Red Lands. The well-exposed Marianna limestone is soft and easily dissolved, so that the surface is much pitted. Humus collects in the pockets, and in the presence of abundant moisture produces a favorable habitat for bryophytes; consequently, almost all the surface of the exposed limestone is covered with liverworts and mosses. Near the main entrance to the extensive Marianna Caverns, *Taxiphyllum mariannae* covers the limestone in large pure mats, but the other mosses usually grow mixed, and as many as five or six different species may be found on a single rock the size of one's hand. *Brachythecium acuminatum* and *Tortula agraria* are the most abundant species on the limestone. Plants of *Gyrowesia Barbula* grow scattered in small pits which they themselves have apparently produced by solution.

Aquilegia australis, *Isopyrum bitematum*, *Podophyllum peltatum*, and *Trillium luteum* are four geographically distinct species of phanerogams absent in the other two regions. The vegetation has a definitely northern aspect, consisting in large part of deciduous trees, and containing probably the lowest percentage of broadleaved evergreens of any region of equal area in the state.

Apalachicola River Bluffs. A narrow strip of rich woodlands extends along the east bank of the Apalachicola River from the Georgia state line south for about eighteen miles. The limestone cliffs, steep bluffs and ravines of this region are of particular interest to botanists because of their two endemic gymnosperms *Torreya taxifolia* (*Tumion taxifolium*) and *Taxus floridana*. *Croonia pauciflora* grows closely associated with *Torreya* (Asa Gray, 1875), as well as several northern species with disjunct distribution. For example, *Syndesmon thalictroides* (*Anemonella*), *Dentaria laciniata*, and *Hepatica triloba* occur nowhere else in Florida, and *Oakesiella floridana*, *Salomonium biflora*, *Uvularia perfoliata*, *Sanguinaria canadensis*, *Trillium Underwoodii*, and *T. lanceolatum* are among the plants whose distribution is phyto-geographically significant (Kurz, 1933).

The restricted region of the Apalachicola River Bluffs has interested botanists since 1833, when Croom discovered *Torreya*. Many botanists have remarked on the extremely limited distribution and endemism of *Torreya* and the interesting northern species associated with it (Croom, 1833-1835; Asa Gray, 1875; Chapman, 1885, 1897; Nash, 1896; Cowles, 1904; Harper, 1914, 1919; and more recently Kurz, 1933, 1938, *et al.*) No adequate explanation has been offered for the peculiar distribution of *Torreya*, since the topography,



Map 1. Regions of endemic species of phanerogams (modified from Harper's map in "Geography and Vegetation of Northern Florida"). Map 2. Two groups of tropical bryophytes from which those occurring in northern Florida have been derived, the Caribbean and the Mexican. Map 3. Distribution of *Brachymerium systylium*, a species derived from Mexico.

geology, and soils vary throughout its range, although the climatic factors are very constant. The simplest and most widely accepted explanation, of course, is that it is a relict species which at one time had a much wider distribution. Mohr (1901) gives the same explanation for the disjunct distribution of *Tsuga canadensis* in northern Alabama.

Eucladium verticillatum forms thick cushions on wet limestone at Aspalaga, almost in the stream, a habitat typical of the species. *Trichostomum jamaicense*, *Fissidens viridulus*, and *Gyroweisia Barbula* occur on drier limestone. *Syrhophodon prolifer*, which covers the sandy soil about the roots of trees in several of the deep shady ravines in the Alum Bluff region, is restricted to the lower levels in which the soil remains constantly moist. *Brachymenium systylium*, *Macromitrium rhabdocarpum*, *Papillaria nigrescens*, and *Platygyrium repens* grow on the bark of decaying logs in damp places, and *Syrhophodon parasiticus* is common on the lower branches of oaks along the rim of ravines. *Schwetschkeopsis denticulata*, *Anomodon attenuatus*, *A. rostratus*, *Haplomenium triste*, and *Thelia asprella*, while not restricted to this region, are conspicuous, the latter especially on the sandy soils at Alum Bluff.

The Tallahassee Red Hills. The Tallahassee Red Hills occupy about three hundred and forty square miles in Leon and Jefferson Counties, and extend a few miles into south Georgia. Although surface soils are red sandy clay, the resemblance to red hills of south Georgia is only superficial, for the two regions are fundamentally different in geology and vegetation. Few surface streams occur since most of the drainage is subterranean, but the several large lakes already mentioned are conspicuous surface features. *Ranunculus palmatus*, *Arisaema triphyllum*, *Sanguinaria canadensis*, *Salomonina biflora*, and *Trillium Underwoodii* are among the interesting disjunct species found here (Kurz, 1928). The three areas containing disjunct species differ in the specific northern relics they harbor, although there is considerable overlapping (Kurz, 1933). No adequate explanation of these differences has been made. Fernald (1937) has called attention to the difficulty involved—and the necessity of caution—in interpreting differences in habitats. Sometimes habitats may be superficially indistinguishable and yet contain different associations of plants.

Jaegerinopsis squarrosa (Britton, 1918b), *Fissidens subcrenatus*, *Microthamnium diminutivum*, *Brachymenium macrocarpum* (Williams, 1913), *Solmsiella Kurzii* (Steere, 1934), and *Dicranella sphaerocarpa* are the significant species in the Tallahassee Red Hills, but they are not found in the other two disjunct areas. The distribution of mosses in the three areas strikingly parallels that of the phanerogams, for each disjunct region has its own particular species which do not occur in the others.

DISCUSSION OF DISTRIBUTION

Species of cosmopolitan distribution. Many species of mosses are more or less cosmopolitan in their distribution, and the general similarity of the moss floras of Florida and of the states farther north is apparent when they are compared. For example, in North Carolina (Anderson, 1938a, 1938b, 1938c,

1939), five hundred miles farther north, more than 50% of the species are common to Florida, and still more remarkable, 20% of the Michigan mosses are the same (Nichols, 1937). Distribution of these cosmopolitan species, especially such weeds as *Funaria hygrometrica* and *Bryum argenteum*, has to a large extent masked the significantly localized distribution of many other species (Steere, 1937a). Little work has been done on the geological history of American species or the identification of regional elements, with the exception of that of Mohr (1901) in Alabama, Evans and Nichols (1908) in Connecticut, Evans (1904, 1906, 1913, 1916a, 1916b, 1922) in New England, Bartram (1928, 1929, 1932, 1934) in Central America and Mexico, Blomquist (1928) in North Carolina, Anderson (1937, 1938a) in North Carolina, and Sharp (1936, 1938a, 1938b, 1939) in the southern Appalachians. A discussion of this problem is found in the paper by Steere (1937b), in which he shows that *Bryoxiphium norvegicum* is restricted to those areas which have escaped glaciation. The many species of mosses of northern Florida which have a restricted distribution fall into two well-defined groups: (1) those occurring more or less commonly in the southern coastal plain, and (2) those not hitherto known in the southern coastal plain.

Species of restricted distribution. Most of the species of mosses found in northern Florida have a more or less widespread distribution in the southern coastal plain. The following species are not restricted to the coastal plain, but occur throughout eastern North America: *Thelia asprella*, *T. hirtella*, *T. Lescurii*, *Climacium Kindbergii*, *Entodon seductrix*, *Pogonatum brevicaulis*, *Desmatodon plinthobius*, *Tortella caespitosa*, *Leucodon julaceus*, and *Trematodon longicollis*. Boreal elements are naturally not conspicuous so far south, but *Aulacomnium palustre*, *Mnium affine*, *Sphagnum subsecundum*, and *S. strictum*, which range as far north as Arctic America, occur in the swamps of the northern part of the state.

Many species occur throughout the southern states, from the Atlantic and Gulf coastal regions through the Appalachian areas and into western Tennessee, Kentucky, and the mountains of Alabama and Georgia. *Schlotheimia Sullivantii*, *Clasmatodon parvulus*, *Funaria serrata*, *Forsstroemia trichomitria* var. *immersa*, *Leptodictyum siphon*, *Physcomitrium turbinatum* var. *Langloisii*, *Fabronia Ravenelii*, *Isopterygium micans*, *Schwetscheopsis denticulata*, and *Fissidens Ravenelii* are typical of this area.

A number of characteristic species have their greatest concentration in the southern coastal plain embracing the Sea Island half of the Atlantic coastal plain and the East-Gulf coastal plain (Fenneman, 1938). Among these are *Syrrophodon floridanus*, *S. texanus*, *Ptychomitrium Drummondii*, *Tetraplodon australis*, *Leucobryum albidum*, *Fontinalis Sullivantii*, *Cryphaea glomerata*, *C. nervosa*, *Bruchia Carolinae*, *B. Donnellii* (Map 4), *Campylopus gracilicaulis*, *Entodon Drummondii*, *Pogonatum brachyphyllum*, *Sematophyllum adnatum*, *Homalotheciella fabrofolia*, *Sphagnum macrophyllum*, *S. henryense*, and *S. cuspidatum* var. *serrulatum*.

Much has been written concerning the distribution of coastal plain species

in the southern Appalachians. Fernald (1931) believes that coastal plain species of phanerogams found along the French Broad River (North Carolina) are probably remnants of a more southern flora, once widely distributed, and not recent invaders. The migration to the coastal plain was in response to the lower temperatures prevailing during the Pleistocene. Sharp (1938b) lists several tropical bryophytes represented in the coastal plain and in the Appalachians; among them are *Entodon Drummondii*, *Leucobryum albidum*, *Fissidens polypodioides*, *Schlotheimia Sullivantii*, and *Syrrophodon texanus*. Since these species are found in or close to areas which have been emergent since the Cretaceous, it seems probable that many of them represent the remains of a once widespread Tertiary flora (Sharp, 1939).

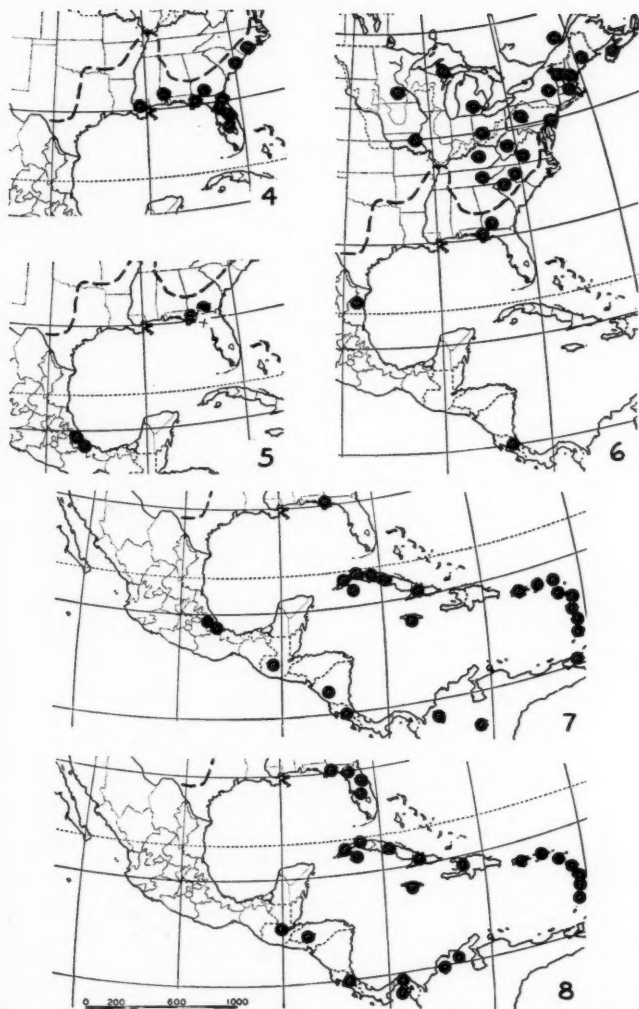
Many typically tropical species reach their northern limits of distribution in the region just north of the Gulf of Mexico. Herzog (1926) calls attention to the enrichment of the bryophyte flora of this coastal region by species of relic character. Fernald (1937) states that a considerable portion of the coastal plain region of Virginia "has the characteristics of either a relic-flora, left over but not dominating in an area from which it has been largely destroyed, or a pioneering flora which has not succeeded in competition with more aggressive and dominating species." A few tropical species which are restricted in northern Florida to the regions known to have been exposed for a long time, and which are rare or absent in geologically new peninsular Florida, are considered relics of a once more abundant tropical flora. *Syrrophodon prolifer* (Map 7), *Solmsiella Kurzii*, *Brachymenium systylium*, and *Fissidens subcrenatus* are good examples. On the other hand, those species which are abundant in the tropics and in southern peninsula Florida but which become rare northward in the state are considered as relatively recent invaders. Many species are included in this category:

Philonotis sphaericarpa (Map 8)
Bryum coronatum
Barbula Cruegeri
Dicranella Hilariana
Syrrophodon parasiticus
S. ligulatus
S. Hobsoni
Cyclodictyon varians

Callicostella pallida
Fissidens Garberi
Microthamnium diminutivum
Octoblepharum albidum
Leucobryum antillarum
Thuidium involvens
Papillaria nigrescens
Tortula agraria

Some of these, such as *Octoblepharum albidum*, *Brachymenium macrocarpum*, *Microthamnium diminutivum*, *Tortula agraria*, and *Fissidens Garberi*, are abundant in the recently exposed Bahamas and Yucatan as well as the young parts of Florida. Amann (1928), in discussing relic floras in Switzerland, states that calciphiles give the impression of being younger species than calcifuges. It is interesting to note that the species here reported for the first time in Florida occur, on the whole, in regions where limestone is exposed. The distribution of such species is apparently dependent upon edaphic factors as much as upon climatic.

Bartram (1932) calls attention to the interlocking distribution of mosses bordering the Caribbean Sea. Examples of this fact may be seen in the rela-



Map 4. Distribution of *Bruchia Donellii*, a typical southern coastal plain species. Map 5. Distribution of *Fissidens subcrenatus*, (●) and *Solmsiella Kurzii* (▲), species of limited occurrence. Map 6. North American distribution of *Haplohymenium trisle*, a species not occurring elsewhere in the coastal plain. Map 7. Distribution of *Syrrhopodon prolifer*, a relic species in northern Florida. Map 8. Distribution of *Philonotis sphaerocarpa*, a species occurring commonly in the American tropics and reaching its northern limits of range in Florida.

tionship of the species collected from Guatemala and British Honduras, which show a close and natural relation to those known from the State of Vera Cruz and Yucatan, with suggestive connections with Antillean and South American species indicated. In two earlier papers (1928, 1929) Bartram discusses the relationship of the mosses of Honduras to those of Mexico and the Antilles, and of those from Costa Rica with South America and to a lesser degree with the Antilles. Steere (1935) lists fifteen species found in Yucatan which are characteristic of the hot lowlands of the West Indies and Central America ("tierra caliente") and which extend into the southern part of the United States and the northern part of South America. In addition to the twelve species from his list which are common to Yucatan and continental Florida the following species from Northern Florida are also widely distributed through the tropical lowlands:

Dicranella Hilariana
D. Herminieri
Philonotis tenella
P. sphaericarpa
P. gracillima
Trichostomum jamaicense
Barbula Cruegeri
Cyroweisia Barbula

Taxiphyllum planissimum
Microthamnium diminutivum
Leucobryum antillarum
Rhizogonium spiniforme
Brachymenium macrocarpum
Fissidens polypodioides
Callicostella pallida
Cyclodictyon varians

As long ago as 1874 Brendel noted that the flora of south Florida served as a link between the floras of North America and the West Indies. A study of the maps of the known distribution of these circum-Caribbean species indicates that most of those found in Florida had their origin in the Antilles, which received many additions, according to Schuchert (1935), from Central America during Miocene and early Pliocene times.

Brachymenium systylium, however, is a characteristic species of Mexico and the southwestern United States, and is a distinctly western element in the Florida moss flora (Map 3). Cardot (1911) relates the moss flora of Mexico to that of the Antilles and Andean regions of Central America and South America, and to that of the United States. This species is representative of the latter group, for it occurs in New Mexico and Arizona as well as in Mexico. Many species are common to Mexico and the southwestern states because of the long extension northward of the Sonoran and Upper Sonoran Life Zones. *Fissidens subcrenatus* is another species found in Florida which occurs at much higher altitudes in Mexico (4500 feet). It is interesting that the Mexican stations for *Brachymenium systylium* and *Fissidens subcrenatus* are in the mountains whereas in Florida they occur only a few feet above sea level. Both areas are characterized by comparatively dry winters and wet summers. The latitude of the Florida stations may compensate for altitude in Mexico. No data on elevation and temperatures for either the Mexican or Florida stations are available. The mountains of southern and central Mexico at altitudes between 4,000 and 10,000 feet have species of flowering plants in common with the southeastern states. It is not strange, therefore, to find species of bryophytes shared by the two areas, since it has been pointed out

that there is a remarkable parallelism between bryophyte and phanerogam floras (Steere, 1927a). Map 2 shows the two groups of tropical bryophytes from which those occurring in northern Florida have been derived.

Fossil flora. Since the present distribution of plants depends upon the character and extent of their past distribution (Harshberger, 1905), any information on past distribution is useful. Fortunately, good accounts of both the fossil fauna and flora of northern Florida exist. Berry (1916) has described twelve higher plants from the Miocene flora of the Alum Bluff formation. Of these the fan palm *Sabalites* is represented in the modern flora by the genus *Sabal*, four genera are now distinctly tropical, one reaches only the Florida keys, and a sixth, although cultivated in northern Florida, is no longer native to the state. Associated with these tropical elements are genera such as *Ulmus*, which is a distinctly temperate genus at the present time.

In discussing this flora Berry states:

The Alum Bluff flora may be considered to be the result of a reversal of the history of the present flora of peninsular Florida. That is to say, the present flora represents primarily a temperate flora receiving additions from the Tropics, whereas the Alum Bluff flora represents an endemic tropical flora gradually becoming invaded by members of a temperate flora as a result of changing climatic conditions.

The region west of the Aucilla River (eastern boundary of Jefferson County) is actually a part of the main continental mass (Vaughan, 1910) and is adjacent to a part of the continent which has not been submerged for a long time. Evidence of this fact may be drawn from the naiad fauna of the Chipola River regions (van der Schalie, 1940), which is rich in endemic forms. Endemic naiads (mussels) are usually found only in regions recognized by geologists and physiographers as having been exposed for much longer periods than more recent surrounding regions where endemism is lacking.

An exact parallel to the situation discussed by Berry and van der Schalie has been discovered in the bryophyte flora. Species whose present distribution is extremely restricted represent apparently the same ancient floristic element as Berry's *Sabalites*, although at the same time other tropical species are migrating northward from peninsular Florida. It is to be emphasized, however, that these two tropical elements are very different in origin and history. Such species of mosses as *Syrrophodon prolifer*, *Brachymenium systylium*, *Solmsiella Kurzii*, and *Fissidens subcrenatus* may be considered relics of a once more abundant tropical flora since they are restricted to these old regions, while *Syrrophodon parasiticus*, *Cyclodictyon varians*, *Callicostella pallida*, *Thuidium involvens*, *Papillaria nigrescens*, *Tortula agraria*, and *Octoblepharum albidum* represent relatively recent invasions.

Species of anomalous distribution. Several species of mosses collected in northern Florida show an extremely limited distribution. *Jaegeriopsis squarrosa* was originally described from Cuba in 1915, has since been discovered in Sanford, Florida, in 1917, in the last two years in two hammocks in northern Florida, and in Puerto Rico. *Fissidens Littlei* was described (as *F. Orcuttii*) in 1927 from material collected near New Orleans, Louisiana, and is still

known only from southern New Mexico and Gadsden County, Florida. *Fissidens subcrenatus* (Map 5) was originally collected at Mirador, Mexico (near Orizaba, State of Vera Cruz), in 1843, was later collected at Jalapa (State of Vera Cruz, Mexico), and has been discovered in Loundes County, Georgia, and about seventy-five miles to the southwest in Leon County, Florida. A fourth species, *Dicranella sphaerocarpa*, was collected in 1908 in Jalisco, Mexico, more recently from Puerto Rico and in Leon County, Florida, and is known only from these three localities. *Solmsiella Kurzii* (Map 5) has been collected only from its type habitat. Further collection may show that the ranges of these species are not actually so discontinuous as they now appear.

Species not occurring elsewhere in the southern coastal plain. Six species of mosses not previously reported in the southern coastal plain have now been collected in northern Florida. These are *Eucladium verticillatum*, *Haplohy-menium triste* (Map 6), *Aphanorrhegna serrata*, *Gymnostomum calcareum*, *Platygyrium repens*, and *Ephemerum serratum*. The only coastal plain station for *Catherinaea crispa* previously reported is in North Carolina. Fernald (1931) has called attention to the derivation of much of the flora of the youthful coastal plain from the ancient Appalachian Uplands. During the colder intervals of the Pleistocene glaciations northern species migrated southward. It seems probable that these typically northern mosses occurring some distance beyond their supposed range represent the remnants of such a southern migration. Brown (1938) states: "It is reasonable to expect that, with the retreat of the ice sheets and the resulting northward migration, some species would persist on favorable sites long after migration." It is significant that these northern species of mosses occur in the regions of disjunct phanerogams in northern Florida, where conditions are favorable for the growth of northern plants.

Geologists, from their studies of that part of the limesink region of central Florida known as "Orange Island," believe that it has been emergent since the Oligocene, when it was separated from the mainland by the Suwannee Strait (Dall, 1892: 111). The general trend of this passage, now occupied by the Okefenokee Swamp and the Suwannee Swamp, followed a line drawn from Savannah to Tallahassee (l.c., 121-122). Paleontological evidence shows that warm tropical waters flowed through the strait, the inner margin of which was considerably north of the Georgia-Florida state line, so that the flora of the bordering land must have been tropical. The Miocene emergence of the northern part of the peninsula connected this island of the Oligocene with the mainland, which allowed migrations northward while a tropical climate still prevailed in the southern part of the United States (St. John, 1936). In discussing the migration of the *Gaylussacia* from South America to North America, Camp (1941b) states that it is becoming increasingly evident that there must have been a much broader land-connection between the two continents than now exists, and that there was a connection during at least part of the Cretaceous between the Atlantic sides of North America and South America in addition to the generally assumed connection on the Pacific side. This connec-

tion, although broken in the Eocene, was partially reformed during the Oligocene. He believes that the Oligocene Island was probably connected with the western portion of Antillia, so that early tropical and subtropical floras could have migrated into the region and thence into their present southeastern coastal plain (Camp, 1941a). At the close of the Oligocene the tropical climate gradually cooled to that of the latitude of present day Chesapeake Bay or Long Island (Vaughan, 1910). Tropical species which once existed throughout the region nearly disappeared, so that at present they remain only as isolated relics in the northern part of the state or in the Orange Island region, the few stations where conditions are still favorable for their growth. Small (1920, 1931, 1938) and St. John (1935) call attention to the fact that a score of native tropical ferns not known elsewhere in the state occur in the Oligocene Island, representing the remains of a very early plant invasion from the American tropics. Any region made up of the oldest and newest geological formations will of course harbor a large number of plants which present interesting problems in distribution. St. John (l.c., 1936) makes the following statement:

During the glacial invasions, or possibly at a later period when the present climatic conditions were established, the great majority of tropical species were exterminated by the colder temperatures as far south as central Florida, as indicated by the great predominance of northern flowering plants at the present time. The tropical ferns that are now isolated in central Florida are the wreckage of the once far richer flora of the Oligocene island.

Fluctuations in sea level have caused shifts in the shore line back and forth across the Floridan Plateau, as the many old beaches and shore lines will witness. Cooke (1939) shows in a series of maps the approximate shore lines of six major levels which have occurred since the beginning of the Pleistocene epoch. During the last of these, the Pamlico shore line stood about twenty-five feet above the present sea level, and the west coast of Florida was broken by many small reentrants into the adjoining higher terraces. Alum Bluff apparently represents the innermost end of one such reentrant, which may account for its significant flora. According to Vaughan the temperature of the water north of Lake Okeechobee was cooler than the tropical water of the Pliocene, but it was still warm. It is therefore reasonable to assume that tropical species may have migrated northward along the warm coastal regions to Alum Bluff.

A few species appear to have found their way into the region from Mexico rather than from the West Indies, as already discussed for *Brachymenium systylum*. The presence of two western species of ferns in the fern grottoes of central Florida indicates that their distribution was once continuous from Florida to Mexico (St. John, 1936). Fernald (1931) calls attention to the presence of a northern remnant of many tropical and austral groups persisting on the young Atlantic coastal plain of the United States, the ancient Greater Antilles, and the ancient Mexican or central American Plateau. The distribution maps of several bryophytes occurring in the southern Appalachians show that these species have much the same Mexican ranges as *Brachymenium systylum* (Sharp, 1939). There is no reason to doubt, therefore, that this species (and others) are of Mexican rather than West Indian origin.

II. List of Species

The nomenclature of the Sphagnaceae follows A. L. Andrews in his revision of the genus in the North American Flora (1913). With a few exceptions the nomenclature of the rest of the Musci follows Brotherus in "Die natürlichen Pflanzenfamilien" (Ed. II, 1924, 1925). Where this treatment differs from Grout in his "Moss Flora of North America North of Mexico" (1928-1940), Grout's name is given in parentheses. Species reported from Florida for the first time by the author (1940, 1941) are marked with an asterisk (*); those reported for the first time for the United States are marked with double asterisks (**).

SPHAGNACEAE

- Sphagnum cuspidatum* Ehrh. var. *serrulatum* Schlieph.
Sphagnum cyclophyllum Sull. and Lesq.
Sphagnum henryense Warnst.
Sphagnum imbricatum Hornsch.
Sphagnum macrophyllum Bernh.
Sphagnum magellanicum Brid.
Sphagnum palustre L.
Sphagnum portoricense Hampe
Sphagnum recurvum Beauv.
Sphagnum strictum Sull.
Sphagnum subsecundum Nees

FISSIDENTACEAE

- Fissidens adiantoides* Hedw.
Fissidens adiantoides Hedw. var. *semicristatus* Grout
Fissidens bryoides Hedw.
**Fissidens Bushii* Card. and Thér.
Fissidens cristatus Wils.
**Fissidens cristatus* Wils. var. *winonensis* (Ren. and Card.) Grout
Fissidens Donnellii Austin
Fissidens Garberi Lesq. and James
**Fissidens Littlei* (Williams) Grout (Moenkemeyera Littlei Williams; *Fissidens Orcuttii* Grout)
Fissidens manateensis Grout
Fissidens minutulus Sull.
Fissidens obtusifolius Wils.
Fissidens polypodioides Hedw.
Fissidens Ravenelii Sull.
Fissidens subbasilaris Hedw.
**Fissidens subcrenatus* Schimp.
Fissidens taxifolius Hedw.
Fissidens texanus Lesq. (*Fissidens viridulus* (Web. and Mohr) var. *texanus* (Lesq.) Grout)
**Fissidens viridulus* (Web. and Mohr) Wahlb.

ARCHIDIACEAE

- Archidium Donnellii* Austin
Archidium floridanum Austin

DITRICHACEAE

- *Pleuridium acuminatum* Lindb.
Ditrichum pallidum (Schrad.) Hampe

DICRANACEAE

- Bruchia carolinae* Austin
Bruchia Donnellii Austin
Bruchia Ravenelii Wils.
Bruchia Sullivantii Austin
Trematodon longicollis Michx.
Dicranella Herminieri Besch.
Dicranella heteromalla (Hedw.) Schimp.
Dicranella Hilariana (Mont.) Mitt.
***Dicranella sphaerocarpa* Card.
Campylopus gracilicaulis Mitt.
Campylopus Donnellii (Aust.) Lesq. and James (*Campylopus gracilicaulis* Mitt. var. *Donnellii* (Aust.) Grout)
Dicranum condensatum Hedw.

LEUCOBRYACEAE

- Leucobryum albidum* (Brid.) Lindb.
Leucobryum antillarum Schimp.
Octoblepharum albidum Hedw.

CALYMPERACEAE

- Syrrophodon floridanus* Sull.
Syrrophodon Hobsoni Hook. and Grev. (*Syrrophodon incompletus* Schwaegr.)
Syrrophodon ligulatus Mont.
Syrrophodon parasiticus (Sw.) Besch.
***Syrrophodon prolifer* Schwaegr. (*Syrrophodon flavescens* C. Müll.)
Syrrophodon texanus Sull.
Calymperes Richardi C. Müll.

POTTIACEAE

- Weisia controversa* Hedw. (*Weisia viridula* Hedw.)
Weisia controversa Hedw. var. *australis* (Austin) Schornherst (*Weisia viridula* Hedw. var. *australis* Austin)
**Gymnostomum calcareum* Nees and Hornsch.

****Cyroweisia Barbula** (Schwaegr.) Paris
(*Desmatodon Barbula* (Schwaegr.) Grout)

***Eucladium verticillatum** (Brid.) Bry. eur.

***Trichostomum jamaicense** (Mitt.) Jaeger
(*Weisia jamaicensis* (Mitt.) Grout)

Tortella flavovirens (Bruch) Broth.

Tortella humilis (Hedw.) Jennings

Barbula Cruegeri Sond.

Acaulon rufescens Jaeger

Desmatodon plinthobius Sull. and Lesq.

Tortula agraria Sw. (*Barbula agraria* Hedw.)

EPHEMERACEAE

***Ephemerum serratum** (Schreb.) Hampe

Ephemerum spinulosum Schimp.

***Ephemerum crassinervium** (Schwaegr.)

C. Müll. var. *papillosum* (Austin) Ren. and Card.

Ephemerum megalosporum (Aust.) Salm.

Nanomitrium Austinii (Sull.) Lindb.

FUNARIACEAE

***Aphanorrhegma serratum** (Hook. and Wils.) Sull.

Physcomitrium turbinatum (Michx.) Brid.

Physcomitrium turbinatum (Michx.) Brid.

var. *Langloisii* (Ren. and Card.) E.G.B.

Funaria hygrometrica Hedw.

Funaria calvescens Schwaegr. (*Funaria*

hygrometrica Hedw. var. *calvescens*

(Schwaegr.) Bry. eur.)

Funaria flavicans Michx.

Funaria serrata Brid.

SPLACHNACEAE

Tetraplodon australis Sull. and Lesq.

(*Tetraplodon pennsylvanicus* (Brid.) Sayre)

BRYACEAE

Pohlia Cruegeri (Hampe) Andrews

***Brachymerium systylium** (C. Müll.)

Jaeger

Brachymenium macrocarpum Card.

Bryum argenteum Hedw.

Bryum capillare Hedw.

Bryum coronatum Schwaegr.

Bryum ventricosum Hedw.

Bryum bimum Schreb. (*Bryum pseudotriquetrum* (Hedw.) Schwaegr.)

MNIACEAE

Mnium affine Bland.

Mnium rostratum Roehl

***Mnium cuspidatum** Hedw.

Mnium punctatum Hedw.

RHIZOGONIACEAE

Rhizogonium spiniforme (Hedw.) Bruch

AULACOMNIACEAE

Aulacomnium heterostichum (Hedw.) Bry. eur.

Aulacomnium palustre (Web. and Mohr) Schwaegr.

BARTRAMIACEAE

Philonotis tenella (C. Müll.) Besch.

(*Philonotis glaucescens* (Hornsch.) Paris)

Philonotis gracillima Angstr.

Philonotis radicalis (Palis.) Brid. (*Phil-*

onotis longiseta (Rich.) E.G.B.)

Philonotis sphaericarpa Brid.

Philonotis uncinata (Schwaegr.) Brid.

ERPODIAEAE

Solmsiella Kurzii Steere

PTYCHOMITRIACEAE

Ptychomitrium Drummondii

(Hook. and Wils.) Sull.

ORTHOTRICHACEAE

Macromitrium rhaddecarpum Mitt.

Schlotheimia Sullivantii C. Müll.

FONTINALACEAE

Fontinalis Sullivantii Lindb.

Brachelyma robustum (Card.) E.G.B.

CLIMACEAE

Climacium Kindbergii (Ren. and Card.)

Grout

CRYPHAEACEAE

Cryphaea glomerata Bry. eur.

***Cryphaea nervosa** (Hook. and Wils.) Bry. eur.

Forsstroemia trichomitria (Hedw.) Lindb.

(*Leptodon trichomitrium* (Hedw.) Mohr)

Forsstroemia floridana (Lindb.) Kindb.

(*Leptodon trichomitrium* (Hedw.) Mohr var. *floridanus* (Lindb.) Grout)

Forsstroemia trichomitria (Hedw.) Lindb.

var. *immersa* (Sull.) Lindb. (*Leptodon*

trichomitrium (Hedw.) Mohr var. *immersus* (Sull.) Lesq. and James)

LEUCODONTACEAE

Leucodon julaceus (Hedw.) Sull.

Leucodon brachypus Brid.

PTEROBRYACEAE

Jaegerinopsis squarrosa E.G.B.

Pirella ludovicica (C. Müll.) Card.

METEORACEAE

Papillaria nigrescens (Sw.) Jaeger and

Sauerb.

HOOKERIACEAE

- Cyclodictyon varians* (Sull.) Broth.
Callicostella pallida (Hornsch.) Jaeger

THELIACEAE

- Thelia hirtella* (Hedw.) Sull.
Thelia asprella Sull.
Thelia Lescurii Sull.

FABRONIACEAE

- **Fabronia Ravenelii* Sull.
Schwetschkéopsis denticulata (Sull.) Broth.
Clasmatodon parvulus (Hampe) Sull.

LESKEACEAE

- Leskea australis* Sharp

THUIDIACEAE

- **Haplophymenium triste* (Cesati) Kindb.
Anomodon minor (Beauv.) Lindb.
Anomodon attenuatus (Hedw.) Hüben
Anomodon rostratus (Hedw.) Schimp.
Haplocladium microphyllum (Sw.)
 Broth. (*Thuidium microphyllum* (Hedw.)
 Best)
Haplocladium microphyllum (Sw.)
 Broth. var. *lignicola* (Kindb.) n. comb.
 (*Thuidium lignicola* Kindb., Ottawa
 Nat. 4:63, 1890; *Thuidium microphyllum*
 (Hedw.) Best var. *ligniculum*
 (Kindb.) Best, Bull. Torrey Bot. Club
 23:88, 1896.)
Thuidium delicatulum (Hedw.) Mitt.
Thuidium minutulum (Hedw.) Bry. eur.
Thuidium involvens (Hedw.) Mitt.

AMBLYSTEGIACEAE

- Campyllum chrysophyllum* (Brid.) Bryhn
Campyllum chrysophyllum (Brid.) Bryhn
 forma *intermedium* Grout
Leptodictyum riparium (Hedw.) Warnst.
Leptodictyum riparium (Hedw.) Warnst.
 forma *obtusum* Grout
Leptodictyum sipho (Beauv.) Broth.
Leptodictyum trichopodium (Schultz)
 Warnst.
Sciaromium Lescurii (Sull.) Broth.
Amblystegium serpens (Hedw.) Bry. eur.
Amblystegium Juratzkanum Schimp.
Amblystegium varium (Hedw.) Lindb.
Amblystegium varium (Hedw.) Lindb. var.
lancifolium Grout

BRACHYTHECIACEAE

- Homalotheciella fabrofolia* (Grout) Broth.
Homalotheciella subcapitillata (Hedw.)
 Card.
Brachythecium Roteanum DeNot.
Brachythecium salebrosum (Web. and
 Mohr) Bry. eur.

Brachythecium acuminatum (Hedw.)

- Kindb. (*Chamberlainia acuminata*
 (Hedw.) Grout)
Cirriphyllum Boscii (Schwaegr.) Grout
Rhynchostegium serrulatum (Hedw.)
 Jaeger (*Eurhynchium serrulatum*
 (Hedw.) Kindb.)
Oxyrrhynchium hians (Hedw.) Loeske
 (*Eurhynchium hians* (Hedw.) Jaeger
 and Sauerb.)
Oxyrrhynchium Rappii Williams (*Eur-*
hynchium Rappii (Williams) Grout)

ENTODONTACEAE

- Entodon seductrix* (Hedw.) C. Müll.
Entodon Drummondii (Bry. eur.) Jaeger

SEMATOPHYLLACEAE

- Sematophyllum adnatum* (Michx.) E.G.B.

HYPNACEAE

- **Platygyrium repens* (Brid.) Bry. eur.
Breidleria arcuata (Lindb.) Loeske (*Hyp-*
num arcuatum Lindb.)
Breidleria arcuata (Lindb.) Loeske var.
americana (Ren. and Card.) n. comb.
 (*Hypnum arcuatum* Lindb. var. *american-*
um Ren. and Card., Bot. Gaz. 14:
 99, 1899).
Isopterygium micans (Sw.) Broth. (*Plag-*
iothecium micans (Sw.) Paris)
Isopterygium micans (Sw.) Broth. var.
latifolium (Grout) n. comb. (*Plagiothec-*
ium micans (Sw.) Paris var. *latifolium*
 Grout, "Moss Flora of North America
 North of Mexico" 3:165, 1932).
Taxiphyllum mariannae (Grout) n.
 comb. (*Plagiothecium Mariannae* Grout,
 "Moss Flora of North America North
 of Mexico" 2:272, 1940).
***Taxiphyllum planissimum* (Mitt.) Broth.
Microthamnium diminutivum (Hampe)
 Jaeger (*Mittenothamnium diminutivum*
 (Hampe) E. G. B.)

POLYTRICHACEAE

- Catherinaea angustata* Brid. (*Atrichum*
angustatum (Brid.) Bry. eur.)
**Catherinaea crispa* James (*Atrichum cris-*
pum (James) Sull.)
Catherinaea Macmillani Holz. (*Atrichum*
Macmillani (Holz.) Frye)
Catherinaea undulata (Hedw.) Web. and
 Mohr (*Atrichum undulatum* (Hedw.)
 Beauv.)
Pogonatum brevicale Brid. (*Pogonatum*
pensilvanicum (Hedw.) Paris)
Pogonatum brachyphyllum (Rich.) Beauv.
Polytrichum commune Hedw. var. *perig-*
onale (Michx.) Bry. eur.

Summary

1. A total of 174 species of mosses has been collected in northern or continental Florida. Of these 22 are new records for the state and four are new to the United States.

2. These species fall into six geographic, or floristic elements, as follows:

- a. species of cosmopolitan distribution.
- b. species characteristic of eastern North America.
- c. species characteristic of the southern states.
- d. species characteristic of the southern coastal plain.
- e. tropical species reaching their northern limits in the Gulf States.
- f. species of anomalous distribution.

3. A definite relation between soils and other ecological factors and the distribution of mosses is shown to exist.

4. Further evidence is given that the distribution of flowering plants is exactly paralleled by that of bryophytes, and that all bryophytes do not have a generalized distribution as commonly supposed.

5. The Oligocene island in central Florida has served as a reservoir of tropical species which migrated northward under favorable conditions.

6. The changing climates of the Pleistocene, in which continental glaciers covered the northern part of North America during maximum refrigeration, attended with long (at least 100,000 years) interglacial periods, may have left its imprint on the flora. This is suggested by the presence of endemic plants of both temperate and tropical alliances, and by the presence of relic and recently arrived species from the tropics and from temperate North America.

7. Relic species of mosses occur in the regions of endemic phanerogams.

8. Those tropical species occurring in northern Florida but absent from southern peninsular Florida are considered as relics of a once widespread tropical flora.

9. Those species of mosses occurring with greatest frequency in southern Florida and the tropics are considered as recent additions to the moss flora of northern Florida.

10. Most of the tropical species found in Florida are typical of the Greater Antilles, whose flora is also related to that of Central America and eastern South America.

11. A few species are typically Mexican rather than West Indian, and must have reached Florida through the southwestern United States.

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DEPARTMENT OF BOTANY,
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A Key to the North American Species of the Genus *Scirpus* Based on Achene Characters

Alan A. Beetle

In recognition of the increased research on seed identification and on animal food habits a key is offered to 45 North American species of the cyperaceous genus *Scirpus* based wholly on characters which may be associated with the achene. At least some members of the genus are common throughout a large part of this region, mostly in wet places, providing both food and shelter for a variety of birds and mammals.

Scirpus setaceus and *S. tuberosus* from Europe are the only introductions. Within their range few of the species are of rare occurrence. Some, e.g. the tulcs, form exclusive colonies over many acres.

In so far as possible size (length and width) measurements have been used, since these characters are not only the least susceptible to varying interpretations but are also least modified during dispersal. Unless otherwise stated length measurements include the apiculate tip (beak) of the achene, and width measurements are taken at the widest point. The figures given indicate the mean of all achenes measured. It is recognized that the variability inherent in *Scirpus* achenes may reach 0.5 mm. from the mean and that places in the key not separated by more than 0.5 mm. difference are correspondingly weak.

The great variability of the achenes in the subgenus *Aphylloides* is counterbalanced by the great uniformity in the subgenus *Euscirpus*. This may indicate that the achene variations are eventually modified by habitat for the plants of the subgenus *Aphylloides* are found in a great range of situations from the arctic to the tropics, from alpine meadows to sea level, and in alkaline to acid soils. On the other hand the species of the section *Euscirpus* tend to inhabit swampy meadows at middle or low elevations in temperate regions.

When color differences are given they always apply to the mature achene. Since the immature achenes frequently pass through white, light brown, gray, or brown stages this is important.

The plates have been drawn by Viola Memmler. They are arranged in the order in which they fall in the key and are numbered according to the alphabetical list that follows the key.

1. A.* 1.5 mm. long or longer (except *S. setaceus* and *S. cernuus* which are 1 mm. long, 0.75 mm. broad); ca. 0.75-2 mm. broad, light to dark brown, gray-brown or black. (Subgenus *Aphylloides* and section *Bolboschoenus* of subgenus *Euscirpus*.)
2. A. not smooth under low magnification.

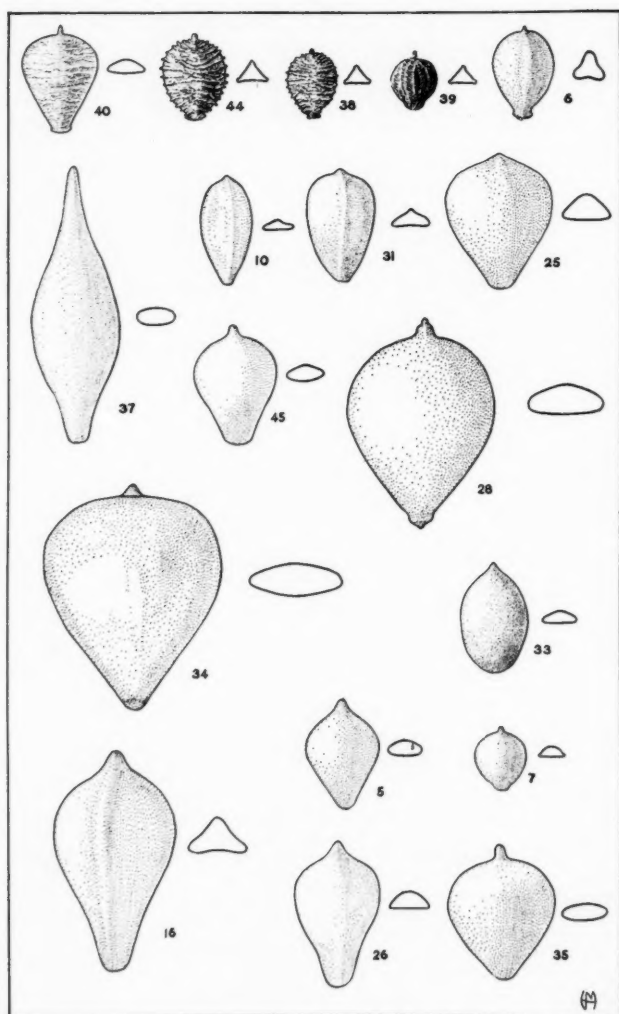
* In order to save space in the key the word achene will be abbreviated as A.

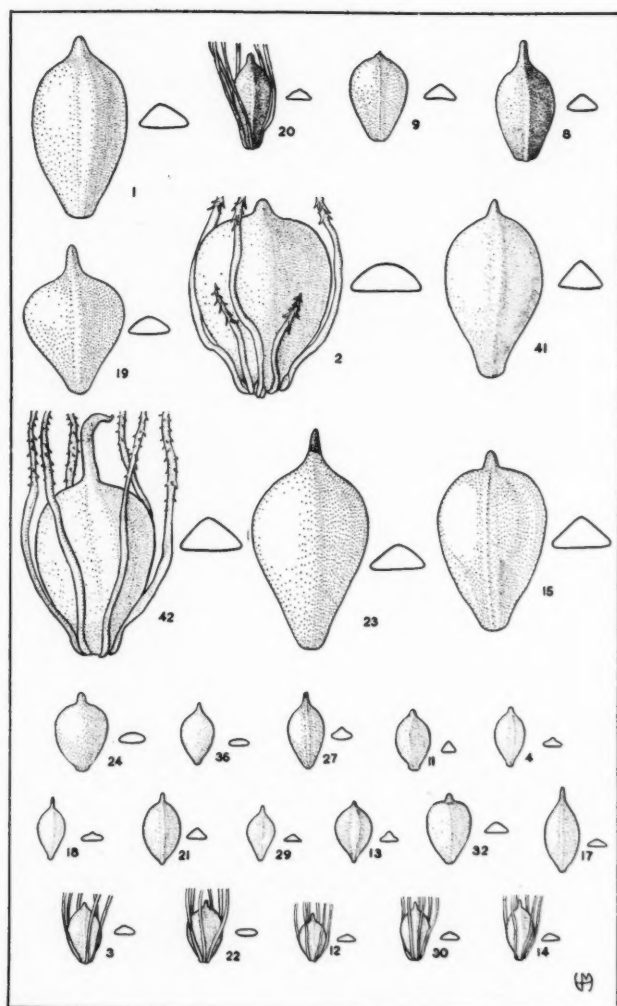
3. A. with prominent ridges vertical39. *S. setaceus*
 3. A. marked with horizontal ridges only, black or blackish (section *Actaeogeton*).
 A. black.
 Horizontal ridges obscure40. *S. smithii*
 Horizontal ridges prominent44. *S. uninodis* var. *hallii*
 A. dark gray-brown38. *S. saximontanus*
2. A. smooth under hand lens magnification.
 4. Constriction at base of A. forming platform6. *S. koilolepis*
 4. Base of A. showing no constriction.
 5. A. 5 mm. long; equally tapered at both ends37. *S. rufus*
 5. A. 4 mm. long, or shorter; obovate or oval.
 6. A. not apiculate.
 A. oval.
 A. light brown10. *S. clintonii*
 A. reddish-brown31. *S. planifolius*
 A. obovate25. *S. nevadensis*
6. A. apiculate, obscurely in some cases.
 7. A. wholly lenticular.
 A. 2 mm. broad.
 Mature A. deep gray45. *S. validus*
 Mature A. brown.
 Apex of A. tapered, bluntly mucronate28. *S. paludosus*
 Apex of A. truncate, minuteley mucronate35. *S. robustus* (incl. var. *novae-angliae*)
- A. 1.25 mm. or less broad.
 A. 2 mm. long.
 A. obscurely apiculate; Canada33. *S. pumilus*
 A. bluntly apiculate, southern U. S. and Central America5. *S. californicus*
7. *S. cernuus*
- A. 1 mm. long7. *S. cernuus*
7. A. plano-convex or compressed to sharply trigonous.
 8. Mature A. gray-brown to black.
 A. 4 mm. long16. *S. fluviatilis*
 A. 3 mm. long.
 A. A. plano-convex26. *S. olneyi*
 A. trigonous.
 A. 2.5-3 mm. long36. *S. rubiginosus*
 A. 2-2.5 mm. long1. *S. acutus*
8. Mature A. light to dark brown.
 9. A. 1 mm. or less wide. Six elongate white bristles persistent about fruit20. *S. hudsonianus*
 Bristles neither elongate nor persistent. Very obscurely apiculate;
 Calif. Sierra Nevada at 10,000 feet9. *S. clementis*
 Prominently apiculate: Greenland and Hudson Bay south to
 N. Carolina in the mountains, scattered in mountains of central
 North America, Washington, north to Alaska8. *S. cespitosus* var. *callosus*
9. A. 2 mm. or more broad.
 Seed coat reticulate veined; body of the achene only 2 mm. long;
 obscurely trigonous19. *S. heterochaetus*
 Seed coat not reticulate; body of A. at least 2.5 mm long; evidently trigonous.
 A. short apiculate, 2.5 mm. long2. *S. americanus*
 A. Long apiculate, at least 3 mm. long.
 A. 3 mm. long.
 A. narrowly ovate, 2 mm. wide41. *S. subterminalis*
 A. broadly ovate, 2.5 mm. broad42. *S. torreyi*
 A. 3.5 mm. long or longer.

- Beak less than 1 mm. long 23. *S. martinus* (incl. var. *fernaldi*)
- Beak more than 1 mm. long 15. *S. etuberculatus*
1. A. usually 1 mm. long and ca. 0.5-0.75 mm. broad, whitish or pale brown at maturity, apiculate, smooth. (Subgenus *Euscirpus* without section *Bolboschoenus*).
10. Bristles neither elongate nor persistent.
11. A. whitish.
- A. lenticular.
- A. oval 24. *S. microcarpus*
- A. obovate.
- Eastern United States 36. *S. rubrotinctus*
- Rocky Mountain region 27. *S. pallidus*
- A. plano-convex.
- Sierra Nevada of California 11. *S. congdoni*
- Eastern United States.
- A. bluntly apiculate 4. *S. atrovirens*
- A. sharply apiculate 18. *S. georgianus*
11. A. light brown.
- A. trigonous.
- A. obovate 21. *S. lineatus*
- A. equally tapered at each end.
- A. 0.5 mm. long 29. *S. peckii*
- A. 1 mm. long 13. *S. divaricatus*
- A. plano-convex.
- A. minutely apiculate 32. *S. polyphyllus*
- A. prominently apiculate 17. *S. fontinalis*
10. Elongate bristles persistent about achene.
- A. whitish 3. *S. atrocinctus*
- A. light to dark brown.
- A. dark brown 22. *S. longii*
- A. light brown.
- A. lenticular 12. *S. cyperinus*
- A. plano-convex.
- Wool whitish brown; central eastern North America, mostly in the interior 30. *S. pedicellatus*
- Wool pale red brown; central eastern N. Am., mostly near the coast 14. *S. eriophorum*

North American Distribution

1. *S. acutus* Muhl.—across Canada from Nova Scotia to British Columbia and south to North Carolina, Tennessee, Oklahoma, Texas, New Mexico, Arizona and California.
2. *S. americanus* Pers.—throughout temperate North America.
3. *S. atrocinctus* Fern.—northeastern United States and Canada, Newfoundland to Saskatchewan, south to Connecticut, western New York and Iowa.
4. *S. atrovirens* Muhl.—Quebec to Saskatchewan, south to Georgia and Missouri.
5. *S. californicus* (Mey.) Steud.—South Carolina and Florida west to California and south to Guatemala.
6. *S. koilolepis* (Steud.) Gleason—across southern United States, Georgia, Kansas and California.
7. *S. cernuus* Vahl—Oregon, California and northern Mexico.
8. *S. cespitosus* L. var. *callosus* Bigel.—Greenland, Labrador, and Newfoundland, south in the mountains to North Carolina; Michigan west to Washington and north to Alaska.
9. *S. clementis* Jones—Sierra Nevada of California at 10,000 feet.
10. *S. clintonii* Gray—Quebec, New Brunswick and Maine west to Minnesota.
11. *S. congdoni* Britt.—California.





12. *S. cyperinus* (L.) Kunth—New England to Virginia, Tennessee and Arkansas.
13. *S. divaricatus* Ell.—Virginia to Florida west to Missouri.
14. *S. eriophorum* Michx.—New Jersey to Florida west to southern Arkansas.
15. *S. eluberculatus* (Steud.) Kuntze—coastal plain, Massachusetts to Florida.
16. *S. fluviatilis* (Torr.) Gray—throughout temperate North America.
17. *S. fontinalis* Harper—Virginia to Florida, west to Louisiana.
18. *S. georgianus* Harper—Quebec to Michigan, south to Georgia and Arkansas.
19. *S. heterochaetus* Chase—eastern Canada, Vermont, New York and Massachusetts; central United States; northern Idaho, Oregon and Washington.
20. *S. hudsonianus* (Michx.) Fern.—Labrador and Newfoundland south to New York, west to Saskatchewan and Montana.
21. *S. lineatus* Michx.—New Hampshire south to Maryland west to Iowa and Alabama.
22. *S. longii* Fern.—Massachusetts and New Jersey.
23. *S. martimus* L. [incl. var. *fernaldi* (Bickn.) Beetle]—Atlantic coast from Nova Scotia to New York.
24. *S. microcarpus* Presl—California north to Alaska, east to Newfoundland.
25. *S. nevadensis* Wats.—Saskatchewan south to Wyoming, west to British Columbia and California.
26. *S. olneyi* Gray—New Jersey south to Florida, west to California.
27. *S. pallidus* (Britt.) Fern.—Manitoba to Kansas and the Rocky Mountains.
28. *S. paludosus* Nels.—on the Atlantic coast from New Brunswick to New Jersey, occasionally inland in Quebec and New York; from Saskatchewan south to Texas and west to the Pacific coast.
29. *S. peckii* Britt.—Connecticut and New York.
30. *S. pedicellatus* Fern.—eastern Quebec to Connecticut, New York, and Wisconsin.
31. *S. planifolius* Muhl.—Maine south to northern Virginia west to Ohio and Missouri.
32. *S. polyphyllus* Vahl—Maine south to Virginia west to Indiana and Tennessee.
33. *S. pumilus* Vahl—Quebec; Saskatchewan; Alberta; Colorado.
34. *S. robustus* Pursh [incl. var. *novae-angliae* (Britt.) Beetle]—Atlantic coast from Nova Scotia to Mexico; California coast.
35. *S. rubiginosus* Beetle—Pacific coast from Vancouver Island to northern Mexico.
36. *S. rubrotinctus* Fern.—Alberta south to Connecticut, New York, the Great Lakes, and Minnesota.
37. *S. rufus* (Huds.) Schrad.—Quebec, New Brunswick, Saskatchewan.
38. *S. saximontanus* Fern.—Ohio; South Dakota south to the Rio Grande; Lower California.
39. *S. selaceus* L.—introduced in northern California.
40. *S. smithii* Gray—Quebec south to northern Georgia and east to Minnesota and western Tennessee.
41. *S. subterminalis* Torr.—Newfoundland south to Virginia west to Washington and Oregon.
42. *S. torreyi* Olney—Maine south to Pennsylvania west to Minnesota.
43. *S. tuberosus* Desf.—near New York, N. Y., and New Orleans, La.
44. *S. uninodis* (Delile) Beetle var. *hallii* (Gray) Beetle—Massachusetts; Florida; Illinois; Missouri.
45. *S. validus* Vahl—throughout central North America.

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Notes on a New Specimen of *Lepidostrobus imbricatus* Hoskins and Cross

J. H. Hoskins and A. T. Cross

Collections of fossil plants from the sandstone rocks of the Pocahontas group (Lower Pottsville) of Orange County, Indiana, are very numerous and have been deposited in various museums throughout the country. Some of these specimens were tentatively or finally identified by the collectors or later workers but the majority of the material has been shelved and essentially forgotten. The most extensive collection, in all probability, is that made by the late David White and described by him in a manuscript which is, unfortunately, as yet unpublished.

One of these very old but undated collections was recently brought to light in some material loaned to the University of Cincinnati by the Cincinnati Museum of Natural History. Among the specimens is a very good strobilus of *Lepidostrobus imbricatus* which we recently described.* The holotype specimen, upon which most of the diagnostic characteristics of the species are based, is a medium sized (13.5 x 2.5 cm.), unflattened, essentially cylindrical, strobilus with the base intact but the tip missing (Fig. 1). The other two smaller specimens which we had at hand at that time are also fragments of the basal portion of the cone only.

The specimen which we recently acquired is from the type locality and is well preserved as a sandstone cast. Only a small portion of the tip of the cone was visible originally, but in our preparation of the material for study we have exposed its entire length and thickness. It is slightly flattened, parallel with the bedding planes of the sandstone matrix. The strobilus is appreciably smaller in all dimensions than the three original specimens and the numerous traces of molds and casts which we found while making our collections. It agrees in all essential details with the holotype. The axis is slightly less than two mm. in diameter constantly throughout its length except for about six mm. of its distal end which tapers very slightly to about one and one-half mm. in diameter. It is bluntly terminated about three mm. from the actual tip of the strobilus (Fig. 2). The sporophylls are spirally arranged, thirteen per revolution about the axis, and the adaxially borne sporangia are densely crowded and distorted. The sporophylls and sporangia are progressively reduced in size throughout the distal cm. of the cone, and the actual bluntly rounded tip of the axis bears extremely shortened and immature sporangia radiating systematically and progressively from the normal position, which is slightly decurrent from horizontal, to a vertical position (i.e., parallel to the cone axis). In gross external appearance, then, the tip of the strobilus is bluntly conical.

*Hoskins, J. H. and A. T. Cross. 1940—Two new species of *Lepidostrobus* from the Lower Pottsville of Orange County, Indiana. Amer. Midl. Nat. 24:421-436.

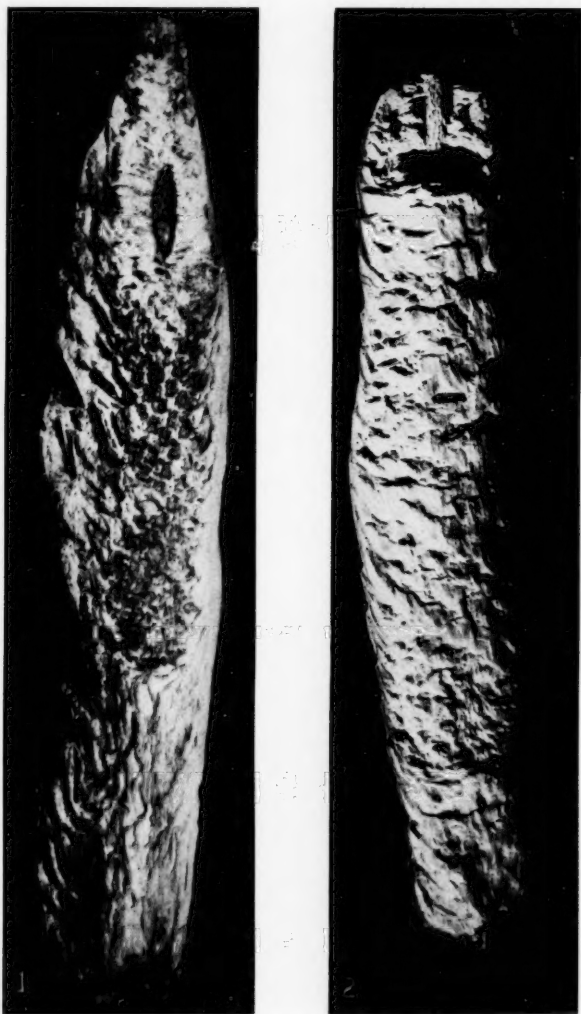


Fig. 1. Holotype specimen of *Lepidostrobus imbricatus*. Base complete and tip missing. $\times 1\frac{1}{8}$.

Fig. 2. Hypotype specimen of *L. imbricatus*. Distal end complete, except for portion broken out to show tip of axis. $\times 1\frac{1}{4}$.

This specimen is designated as a hypotype of *Lepidostrobus imbricatus* since it has made possible the revision of the original description.

The emended type diagnosis follows:

***Lepidostrobus imbricatus* (Hoskins and Cross) emend.**

Strobilus: Medium size, more than 13.5 cm. long by 1.8-2.5 cm. in diameter, essentially cylindrical, base (proximal end) not tapered, tip slightly tapered and bluntly conical. Specimens preserved as fine sandstone casts.

Axis: Approximately 4-5 mm. in diameter at base, tapered abruptly to 2-3 mm. throughout the remainder of length except the distal end which tapers very slightly to the blunt, rounded tip. 13 sporophyll bases prominent when viewed in cross section. No cellular detail observed.

Sporophylls: Arranged spirally, 13 per revolution about the axis and approximately 5 revolutions per cm., progressively reduced in size and maturity at the immediate distal end and so arranged as to form a bluntly-conical tip. Pedicels inserted at right angles to axis and about 6-8 mm. in length to the distal ends where laminae curve evenly upward. No subtended or thickened portion of lamina evident. Laminae 1.5-2.0 cm. long, slender, not over 1.5 mm. wide at base, tapering gradually to sharp point, closely appressed, overlapping many laminae above, imbricate in appearance. Median nerve is prominent.

Ligule: Definite evidence lacking, possibly because of imperfect preservation.

Sporangia: Borne adaxially on sporophyll pedicel. Greatly elongated (6-8 mm.), wedge-shaped in top view, wedge-shaped in cross-section near axis but broadly flattened at distal end and overlapping narrower sporophyll; attachment not distinguishable. Densely crowded vertically and laterally and thus distorted. Immature at tip of strobilus.

Spores: Small (26.5μ), triradiate openings in some; obtained only by maceration. No larger spores found in this strobilus.

Location and horizon: Pocahontas sandstone, Lower Pottsville series, Pennsylvanian system. Six miles northwest of Orleans, Orange County, Indiana; Chailleux quarries.

Number of specimens: Four. One fairly complete strobilus, the holotype specimen, with base intact; one slightly smaller specimen with tip intact, the hypotype specimen; two smaller fragments; several traces of other strobili of probably the same type. Holotype, No. B-620 and hypotype, No. B-1981; Paleobotanical Museum, Botany Department, University of Cincinnati.

Name of species: *Lepidostrobus imbricatus*, after the imbricate nature and appearance of the laminae of the sporophylls.

Notes and Discussion

Lepidostrobus aristatus Hoskins and Cross, a homonym

J. H. Hoskins and A. T. Cross

Paleobotanists frequently encounter a multiplicity of names while classifying new material, the study of which necessitates either a combination or segregation of organ genera. In the subsequent revision whole groups of valid species names may fall into synonymy. For example a large number of cone genera has been proposed for the fossil lycopods. Some of these such as *Lepidostrobus*, *Lepidocarpon*, and *Lepidophyllum* are well known, although their exact generic limitations and relationships are not clear. Therefore when new names are to be applied in these genera to species believed to be valid, it is expedient to avoid any repetition of specific names already used in closely allied genera, regardless of whether these genera are based on the same or different organs of closely related plants. Such reasons are largely responsible for the fact, that the name given by us to a fructification from the Pottsville sandstone of Orange County, Indiana, *Lepidostrobus aristatus* Hoskins and Cross, 1940, is preoccupied.

In 1873, Newberry¹ described a new genus, *Polysporia*, with one species, *P. mirabilis*. Later Lesquereux² referred this genus to *Lepidostrobus*. This specimen, which is undoubtedly a portion of a cone of *Lepidostrobus* showing large numbers of microspores in club-shaped sporangia, is recognized as a good species, *Lepidostrobus* (*Macrocystis*) *mirabilis* (Newby.) Lesqx.

In 1914, Nathorst³ described *Lepidophyllum mirabile*. Bassler⁴ created the new genus *Cantheliophorus* in 1919 and assigned to it seven new species and five others previously described in other genera, among them Nathorst's *L. mirabile*. Jongmans and Gothan⁵, doubting the validity,⁶ reassigned the species to *Lepidophyllum* (*Cantheliophorus*) *mirabile* Nathorst. But *Lepidophyllum* as a genus appears to contain sporophyll fragments of cones readily referable to species of *Lepidocarpon*, or sometimes *Lepidostrobus*, which have already been described. Therefore, as Jongmans⁷ points out, *Lepidostrobus* (*Macrocystis*) *mirabilis* (Newby.) Lesqx. has priority over Nathorst's name, regardless of whether it is a *Lepidophyllum* (*Cantheliophorus*) or a *Lepidostrobus*. He then proposes a new name, *Lepidophyllum* (*Lepidostrobus*) *aristatum* Jongm. for this material.

Since *L. aristatus* is preoccupied, we propose here the name *Lepidostrobus arrectus* Hoskins and Cross, nom. nov., for our species.⁸ Although the attenuated laminae of superimposed sporophylls overlap, these laminae are not closely appressed; rather they arise at angles of 70°-80° from the pedicels. The name *arrectus* refers to this condition.

1 Newberry, J.S. 1873—Fossil Plants. Geol. Rept. of Ohio. Geol and Paleont. I, Part II, Paleontology, Sec. III: 360-62, pl. 41, figs. 5, 5a and 6.

2 Lesquereux, Leo. 1879—Coal flora of Pennsylvania. Second Geol. Surv. Penn. 2:443-446.

3 Nathorst, A. G. 1914—Zur Fossilen Flora der Polarländer. I, 4: 63, pl. 13, figs. 19-30, text-fig. 16.

4 Bassler, Harvey. 1919—A sporangiophoric lepidophyte from the Carboniferous. Bot. Gaz. 68:73-108, pl. 10, figs. 22-24.

5 Jongmans, W. J. and W. Gothan. 1925—Geol. en Paleontol. Beschrijving Karbon van Epen. Mededeel. No. 1. Geol. Bur. Nederl. Mijnged. Heerlen, Jaarverslag 1925: 69, pl. 11, fig. 14.

6 Schopf, James M. 1941—Notes on the *Lepidocarpaceae*. Amer. Midl. Nat. 25: 548-563. (Schopf here gives adequate reasons for referring the American forms named *Cantheliophorus* to *Lepidocarpon*).

7 Jongmans, W. J. 1930—Einige Namenänderungen bei *Lepidostrobus*. Geol. Bur. Nederl. Mijnged. Heerlen, Jaarverslag 1930:87-92.

8 Hoskins, J. H. and A. T. Cross. 1940—Two new species of *Lepidostrobus* from the Lower Pottsville of Orange County, Indiana. Amer. Midl. Nat. 24:421-436.

Book Reviews

FARLOWIA. A Journal of Cryptogamic Botany. David H. Linder, Editor. Published by Farlow Library and Herbarium of Harvard University, Cambridge, Mass. Vol. I, No. 1, January 1943, 170 pp., 16 pls., 1 fig. Single numbers \$1.50 each, subscription per volume \$5.00.

While the appearance of any new scientific journal is a noteworthy occasion, the publication of the first issue of *Farlowia* is doubly auspicious. The few existing journals of cryptogamic botany, almost exclusively European, are no longer available and must probably be added to the list of minor casualties. On the other hand no exclusively cryptogamic journal, ranging from the algae to the bryophytes, has ever been published in America.

Although *Farlowia* is to take the place of the *Contributions from the Cryptogamic Laboratory and the Farlow Herbarium* (No. 225 will complete Vol. nine), contributions from the outside are invited by the editorial board made up of ten members in addition to the Editor. As individual volumes are to consist of four semi-annual issues of about 125 pages each, Volume one will fittingly come to a close in 1944 marking the 100th anniversary of the birth of William Gilson Farlow.

The issue on hand contains nine papers, two of which deal with algae, two with mosses and five with fungi. The Editor's Foreword is an eloquent defense of taxonomy in general and that of cryptogams in particular in the event that numerous other and perhaps equally important reasons should fail to justify the new venture at the present time. No geographical limits are imposed on contributors. However, the very liberal upper limit of 100 printed pages has been set for any one article. The accepted policy of compliance with the International Rules is as commendable as are the excellent typography, illustrations and careful editorial work.

Farlowia is the obvious and welcome expression of the increasing importance of and interest in cryptogamic botany in the United States and as such deserves the whole-hearted support of all botanists.—THEO. JUST.

COMMON EDIBLE MUSHROOMS. By Clyde M. Christensen, The University of Minnesota Press, Minneapolis, 1943. x + 124 pp., 4 colored plates, 62 figs. \$2.50.

Despite the appearance in recent years of a number of books and pamphlets on edible mushrooms, the attitude of the American public toward these interesting dietary adjuncts has been largely apathetic. The very real and serious consequence of making a mistake has undoubtedly deterred many who might otherwise have been interested from experimenting with them. It is not unlikely that the stress of a war-time economy may do a great deal to stimulate the desire for information on the subject.

The author of the book here considered has wisely refrained from attempting to describe all mushrooms, restricting himself to an attempt to indicate clearly and unmistakably a limited number of edible forms, and, as a warning, the relatively few, but sometimes common dangerous species. He gives particular attention to what he calls "the fool-proof four": the morels, the puffballs, the shaggy-manes and the sulphur polypore. He emphasizes repeatedly that it is better to learn to distinguish accurately a few common species, gradually and cautiously enlarging one's acquaintance, than to indulge in indiscriminate mycophagy. About fifteen pages are devoted to directions for cooking mushrooms.

Except for serious confusion on page 12, for which the printer is obviously to blame, the text is clear and written in attractive style. If the nomenclature adopted is somewhat obsolete, this is perhaps an advantage rather than otherwise in a book intended for popular use. The half-tones are in general excellent. The four colored plates, illustrating eighteen species, are not quite so successful, but their shortcomings are not such as to

lead to dangerous error. The giant puffball has never been reported as "5 feet high." The inclusion of *Lenzites betulina* and *Panus rudis* among the edible forms is somewhat surprising and may result in discouraging some would-be mycophagists and there will be dissent from some evaluations of relative merit, but these things are, after all, matters of individual taste.

The book promises to be both useful and timely and should serve to introduce the common edible mushrooms to many who do not yet know and enjoy them.—G. W. MARTIN, State University of Iowa.

GUIDE TO THE LITERATURE OF THE ZOOLOGICAL SCIENCES. By Roger C. Smith. Burgess Publishing Co., Minneapolis, Minn. 1942. vii + 128 pp. \$2.00.

Among other prerequisites successful research includes an adequate knowledge of the literature available in the particular field. In most cases this literature is extensive and difficult to reach without proper training or assistance. Written to serve this end, the *Guide* represents the outgrowth of a course taught by the author for a number of years and designed to prepare students for the complicated task of solving their own problems of scientific literature. Professional zoologists, too, will find it a handy source of very useful information. Its publication makes zoological literature almost as accessible as that of chemistry with its excellent guides.

The *Guide* covers all important topics such as systems of library classification, review and abstracting journals, reference works, dictionaries, methods of bibliography, the preparation of scientific papers and illustrations, and contains many problems for the student. The text is usually concise, informative, reliable and is marred by few typographical errors. It is unfortunate, however, that some titles are misleading, e.g., on p. 47 the *Internationale Revue der Geschichte Hydrobiologie und Hydrographie* (sic) is characterized as a journal which "reviews the literature and lists references on aquatic problems." The lists of foreign and domestic abstracting and reviewing journals could profitably be amended by the addition of the following titles: *Isis* (devoted to the history of science), *L'Année Biologique*, *Bibliographia Biotheoretica*, *Botanical Review*, *Fortschritte der Zoologie* (new series), *Zeitschrift für wissenschaftliche Mikroskopie*, etc. On p. 93 G. H. F. Nuttall's *Notes on the Preparation of Papers for Publication in the Journal of Hygiene and Parasitology* (Cambridge, 1940) might be added in view of their general usefulness. Of reference works not listed *Rabenhorst's Kryptogamen-Flora* might be useful to the protozoologist or the limnologist, and the paleontologist may wonder why the *Fossilium Catalogus* was not included here. However omissions of this kind should not deter the reader from using this eminently practical and informative *Guide*.—THEO. JUST.

CANADIAN FISHERIES MANUAL—1942. The Story of Canada's Fishing Industry. By Frederick William Wallace. National Business Publications, Gardenvale, Quebec. 1942. 1-102 + 1-116 pp. plates, figures. \$3.00.

This factual well-illustrated story by fishermen about fish and fishing is directed to laymen, students, and teachers who may desire a reference book on the fishes, fishing grounds, methods of fishing, preparation of fishes for market, and economic importance of the Canadian commercial fisheries. The few shortcomings of the volume, such as the unrevised scientific names, are heavily outweighed by its general value. The profusion of clear photographs of production and processing deserves especial mention. The high quality of the sponsors' part of the book, consisting of full-page displays of historical and current methods of operation, is more informative than some parts of the text, and sets a new peak in dignified and instructive merchandising. The fishes of the Great Lakes receive their due share of attention, with short notes on the habits of several of the most important species.—KENNETH H. DOAN, F. T. Stone Laboratory, Ohio State University, Put-In-Bay, Ohio.

